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BEHAVIOR AND ECOLOGY OF HARBOR SEALS (PHOCA VITULINA RICHARDSI) INHABITING GLACIAL ICE IN AIALIK BAY, ALASKA

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BEHAVIOR AND ECOLOGY OF HARBOR SEALS

(*PHOCA VITULINA RICHARDSI*)

INHABITING GLACIAL ICE IN AIALIK BAY, ALASKA.

A

THESIS

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Agnes Anne Hoover, B.A.

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BEHAVIOR AND ECOLOGY OF HARBOR SEALS

(PHOCA VITULINA RICHARDSI)

INHABITING GLACIAL ICE IN AIALIK BAY, ALASKA.

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ABSTRACT

Harbor seals (*Phoca vitulina richardsi*) in Aialik Bay, southcentral Alaska, haul out on glacial ice calved from Aialik Glacier. Abundance, distribution, and behavior of seals were recorded in relation to environmental variables between mid-May and mid-August 1979-1981.

The number and age composition of seals on the ice varied daily and seasonally. Maximum numbers were counted during June (pupping) and August (molting). In June, 60%-90% of the seals were adults, while in August, 80% were subadults. Fewest seals, mostly subadults, were counted in July, the breeding season. Seal abundance on ice was highest in midday, especially for two days following storms; fewest seals were on the ice at night, during the day preceding a storm, or during foul or windy weather. Tides had little effect on numbers. The degree of gregariousness and time of hauling out varied seasonally and with the seals' age and reproductive condition.

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TABLE OF CONTENTS

Abstract 3

Acknowledgements 4

List of Figures 7

List of Tables 9

Introduction 11

Literature Review 16

Habitat Types and Haul-out Patterns 16
Life History 21
Feeding Habits 24

Study Area 27

Methods 32

General Surveys 32
Aialik Bay Studies 32

Censusing 33
Abundance Rank 36
Weather 37
Tides 38
Ice Classification 38
Age Composition 39
Group Density 40
Habitat Use 42
Parturition 42
Trawl Samples 43
Statistical Analysis 43

Results 47

Distribution and Movements 47
Haul-out Schedule 49

Diel Activity Cycle 51
Influence of Weather 51
Tidal Influences and Dispersion of Ice 58
Multivariate Analysis 63

Population, Life Cycle, and Social Behavior 66

Age Composition 66

Natality 69
Characteristics of Haulout Sites 77
Pup Mortality 89
Breeding Behavior 92
Molting 95

Potential Prey 98

Discussion 102

Population Assessment 102
Comparative Ecology of Aialik Bay Harbor Seals 106

Timing of Parturition 107
Use of Habitat 111

Selective Advantages of Ice as a Haulout Substrate 116

Summary 120

References 125

LIST OF FIGURES

Page

Fig. 1. Southern part of the Kenai Peninsula................. 28

Fig. 2. Map of upper Aialik Bay............................ 29

Fig. 3. Harbor seal study area in upper Aialik Bay. 34

Fig. 4. Classification of groups of harbor seals on the basis of numbers and density. 41

Fig. 5. Example of distribution of ice which limited the number of seals able to haul out in Aialik on 23 May 1980. 48

Fig. 6. Variation of daily maxima in censuses of harbor seals on the ice in upper Aialik Bay, spring and summer, 1979-1981. 50

Fig. 7. Relationship between time of day and abundance of harbor seals on the ice in Aialik Bay, 1979-1981. 52

Fig. 8. Examples of diurnal variation in the abundance of 7- to 8-okta (black), 4- to 6-okta (diagonal), and 3-okta or less (clear) ice in Aialik Bay, 1980. 53

Fig. 9. Relationship between weather and harbor seal abundance on ice in Aialik Bay, 1979-1981. 54

Fig. 10. Abundance of harbor seals hauled out in relation to storms in Aialik Bay, 1979-1981. 56

Fig. 11. An example of the effect of strong northwesterly winds on the number of harbor seals hauled out in Aialik Bay, 26-27 May 1979. 57

Fig. 12. Relationship between tidal stage and harbor seal abundance in Aialik Bay, 1979-1981. 62

Fig. 13. Seasonal fluctuations in the relative age composition of seals in upper Aialik Bay, 1979-1980. 67

Fig. 14. Seasonal fluctuations in the midday counts of adult harbor seals with pups and without pups and of subadults in Aialik Bay, 1980. 68

Fig. 15. Frequency of occurrence of births of harbor seals in upper Aialik Bay, 1979-1981. 70

Page

Fig. 16. Seasonal variation in daily abundance of unweaned harbor seal pups in upper Aialik Bay, 1979-1980.. 73

Fig. 17. Diurnal variation in birth rates of harbor seals in upper Aialik Bay, 1979-1981...................... 74

Fig. 18. Seasonal variation in daily abundance of weaned harbor seal pups in upper Aialik Bay, 1979-1980..... 76

Fig. 19. Surface diameter of bergs used as haulout sites by three reproductive classes of harbor seals in Aialik Bay, 1980................................ 78

Fig. 20. Comparative distances between bergs occupied by harbor seals of three reproductive classes in Aialik Bay, 1980................................. 79

Fig. 21. Comparative densities of ice used by harbor seals of three reproductive classes in Aialik Bay, 1980...................................... 81

Fig. 22. Seasonal variation in the proportion of females with pups sharing bergs with other seals in Aialik Bay, 1980................................. 83

Fig. 23. Seasonal variation in the ice cover surrounding haulout sites during early pupping, post-partum suckling, breeding and molting in Aialik Bay, 1980.. 87

Fig. 24. Seasonal variation in percent of area north of Slate Island covered by 7- to 8-okta ice during 1979. Open circles represent ice cover during times of strong northwesterly winds. The small graph shows seasonal variation in frequency of occurrence of strong northwesterly winds along the Kenai Peninsula (Brower et al. 1977).......... 88

Fig. 25. Seasonal fluctuations in the number of pups less than three weeks old that were unaccompanied by their mother in Aialik Bay, 1979-1980.............. 90

Fig. 26. Seasonal variation in the proportion of unmolted (0% molt) seals and seals in early stages of hairloss (1-50% molt) sighted on the ice in upper Aialik Bay, 1980............................ 97

Fig. 27. Clinal variation in the timing of parturition in harbor seals in the North Pacific region........... 108

LIST OF TABLES

Page

Table 1. Environmental parameters associated with peak abundance of harbor seals in the western North Pacific... 19

Table 2. Prey of harbor seal pups in Alaska.................. 26

Table 3. Epibenthic and mid-water trawls taken in Aialik Bay, 1979-1982.................................... 44

Table 4. Direction and rate of ice movement relative to tidal stages in Aialik Bay, 1979-1981................ 59

Table 5. Time of day and direction of ice movement relative to tidal stages in Aialik Bay, 1979-1981.. 61

Table 6. Contingency table used for multiway frequency table analysis of the relationship between seal abundance, time of day, weather, and tidal stages in Aialik Bay, 1979-1981..................... 64

Table 7. Summary of results from the multiway frequency table analysis of the relationship between seal abundance, time of day, weather, and tidal stages in Aialik Bay, 1979-1981..................... 65

Table 8. Numbers of adult- and subadult- size females with pups sighted during early (22-28 May) and late (2-8 June) peaks of pupping in Aialik Bay, 1981.. 72

Table 9. Variation in the proportion of each age/sex class observed on bergs with other seals in Aialik Bay, 1980................................. 82

Table 10. Comparison of age-composition of seals sharing bergs with females and pups with that of the population as a whole in Aialik Bay during three time periods in 1980......................... 84

Table 11. Variation in group density relative to time for seals with and without pups in Aialik Bay, 1980.. 86

Table 12. Potential prey of harbor seals observed and collected in upper Aialik Bay, 1979-1982............ 100

Table 13. Comparison of the timing of parturition for three pupping areas in the Gulf of Alaska........... 109

Page

Table 14. Duration of suckling for phocid seals on land and on ice in the North Pacific region.............. 115

INTRODUCTION

Ecologically, the Pacific harbor seal (*Phoca vitulina richardsi*, Gray 1864) is a generalist, occupying a diverse array of nearshore habitats in temperate and subarctic waters. The range of harbor seals in the Pacific Ocean includes the shoreline and nearshore islands from San Ignacio Lagoon, Mexico (27° N) northward through southeastern Alaska, westward into the Bering Sea, Aleutian, Commander, and Kuril Islands, and southward to Hokkiado, Japan (43° N). Haulout areas extend to Nunivak Island and western Kamchatka (63° N), while pupping colonies extend as far north as Kuskokwim Bay (59° N) and Prince William Sound (61° N), Alaska (Johnson 1976a, Shaughnessy and Fay 1977, Burns and Gol′tsev, in press, F. H. Fay, pers. comm., J. J. Burns, unpub. data). Although typically found in coastal waters within 20 km of shore, harbor seals show pelagic tendencies, occasionally ranging out to 100 km offshore. They also frequent freshwater streams and lakes (Pitcher and Calkins 1979, Everitt and Braham 1980, Bigg 1981). Habitats used for haulout include cobble and sand beaches, tidal mud flats, offshore rocks, glacial and sea ice, and man-made objects such as piers and log booms (Bishop 1967, Johnson 1976a, Calambokidis *et al*. 1978, Pitcher and Calkins 1979, F. H. Fay pers. comm.).

The number of harbor seals inhabiting the North Pacific is unknown. This is primarily a result of the seals′ scattered distribution and our limited ability to sight seals in the water (e.g., Dohl 1978) or estimate the proportion of seals hauled out.

Estimates of the number of harbor seals along the eastern shore of the North Pacific Ocean range from 50,000-200,000 (Scheffer 1958). More recent surveys estimate a minimum population size of 315,000 (Bigg 1969b, Mate 1977, Dohl 1978, 1980, Everitt and Braham 1980).

Estimates of the number of harbor seals inhabiting a particular area are important for several reasons. Harbor seals were hunted for bounty in order to reduce competition with nearshore fisheries for prey of commercial value (Imler and Sarber 1947, Everitt 1980). Hunting pressure increased as the pelts became more valuable. Commercial hunting of seals was later banned with the passage of the Marine Mammal Protection Act of 1972. The potential impact of seals on fisheries once again has become a matter of increasing concern (Matkin and Fay 1980, Everitt 1980). Potentially extensive offshore oil development may pose a threat to the community in which the harbor seal is a top level consumer (Pitcher and Calkins 1979). Several major studies have been conducted in order to assess the potential impact of offshore oil development on the marine environment (e.g., Outer Continental Shelf Environmental Assessment Program). Boating activities and onshore development, such as logging and homesite construction, have been encroaching on harbor seal habitats. Several studies have been conducted to address the effects of nearshore human-caused disturbances on seal activities (e.g., Hazard 1977, Calambokidis et al. 1978, Allen et al. 1979, Murphy and Hoover 1981). Recently, Federal agencies have placed an emphasis on modeling various marine ecosystems in order to assess the impact of human-related disturbances on the environment. To develop those models and assess the impact of human activities on seal populations, methods for determining the magnitude of seal populations along the coast must be developed.

The mobility and behavioral flexibility of harbor seals are such that current survey methods for censusing the seals are insufficiently refined to detect any but very large changes in their abundance. This is largely due to insufficient knowledge of the activities of seals under different seasonal and regional conditions, as well as to a lack of standardization of methods for studies of the main environmental parameters that affect their activity.

Phocid seals use two primary types of substrates for haulouts: ice and shore. The life-history strategy of seals using ice tends to differ markedly from that of seals using the shore (Burns 1970, Stirling 1975). Stirling (1975) and Le Boeuf (1979) have proposed that social differences between pagophilic ("ice loving") and pagophobic ("ice fearing") seals during the pupping and breeding seasons are at least partially attributable to characteristics of their respective habitats. Seals that haul out on land often are spatially confined. Their access to haulouts is limited, and because the seals have restricted mobility on land, they tend to remain near the access points. Thus, pagophobic seals tend to haul out in dense clumps. Conversely, seals that haul out on ice have unlimited access points and tend to be more dispersed. Due to climatic variation, pack ice is less predictable than land in location and quality; however, the vast surface area available to the seals removes any spatial constraints which might force them to aggregate in dense clumps (Fay 1974). During the pupping and breeding seasons, pagophilic seals usually are found singly or in low density aggregations, widely spaced over suitable habitats (Burns 1970, Fay 1974). The densities of those aggregations, especially for pupping, have marked effects on the type of breeding behavior exhibited (Bartholomew 1970, Stirling 1975, Le Boeuf 1979).

This information is essential for those conducting systematic aerial and boat surveys. The study reported here was of a population of harbor seals that congregates on glacial ice in Aialik Bay (59°56′N, 149°43′W). Glacial ice is a substrate that is intermediate in some qualities between sea ice and shores. In spring, haulout space on glacial ice is abundant throughout the day and access points are unlimited. Unlike sea ice, however, glacial ice is less extensive, hence it does not allow seals to disperse to the degree possible on sea ice. Also, its location is predictable, like that of haulouts on shore, allowing the seals to anticipate the location of other resting seals.

If the limited space on terrestrial haulouts does restrict the social flexibility of seals, as inferred by Stirling (1975) and Le Boeuf (1979), one might expect the harbor seals occupying glacial ice to be less gregarious than those on shore and perhaps more inclined to segregate by age and sex. On glacial ice, seals have a better opportunity to select their companions. Seals on shore are limited by both the location of haulouts and the access to them. Because movements are more limited on shore, seals which haul out there may select resting sites where they are tolerated by neighboring seals (Knudtson 1974, Sullivan 1979). On the other hand, seals hauling out on ice have unlimited access to haulout sites and are able to select which seal, if any, they will haul out near.

The objective of this study was to examine some of the effects that glacial ice as a haulout has on the life-history of the Pacific harbor seal. I determined basic life-history parameters for seals on glacial ice and compared those with parameters reported in the literature for harbor seals hauling out on shore. Aggregational characteristics also were compared to examine the hypothesis that seals using glacial ice show significant differences in group structure from those hauling out on land, as predicted by Stirling (1975) and Le Boeuf (1979).

I use the term "pagophilic" to refer to seals hauling out on sea ice when pupping and breeding and "pagophobic" to refer to those hauling out on shore. Although harbor seals pupping on glacial ice clearly are "ice loving", I distinguish them as "glacial" seals because of the intermediate characteristics of their habitat.

LITERATURE REVIEW

Studies of harbor seals using glacial ice as a haulout substrate were conducted previously by Bishop (1967), Pitcher and Calkins (1979), and Streveler (1979). Bishop (1967) examined the behavior and reproductive biology of seals in the glacial fjords of Aialik and adjacent Harris Bays, as well as on the beaches of Tugidak Island, Alaska. Pitcher and Calkins (1979) examined the biology of harbor seals throughout the Gulf of Alaska, including those in several fjords with tidewater glaciers. Streveler (1979) examined the distribution and population ecology of harbor seals in Glacier Bay National Monument.

Habitat Types and Haulout Patterns

In selecting a haulout site, harbor seals appear to choose those having protection from predators approaching from the landward side, direct access to deep water, and proximity to food (Scheffer and Slipp 1944). They also appear to select sites having protection from strong winds and high surf such as in bays, inlets, and fjords (Hazard 1977, Sullivan 1980, Burns and Gol′tsev in press). They are least abundant on simple, exposed coasts (Fisher 1952, Hazard 1977, Everitt and Braham 1980, Sullivan 1980, Burns and Gol′tsev in press). Burns and Gol′tsev (in press) observed that seals in the Aleutian Islands tended to use narrow boulder beaches and nearshore rocky islands in protected waters, whereas along the more exposed coastlines they tended to haul out on wider, gently sloping beaches. On Tugidak Island, the seals haul out on smooth beaches, lacking large rocks or beach-cast debris. When those beaches with high bluffs are unavailable, due to heavy surf, the seals haul out on exposed spits and bars (Bishop 1967). Harbor seals tend to use sand and mud bars only where such habitats are adjacent to deep channels which provide access to open water (Johnson 1976a, Calambokidis *et al.* 1978, Sullivan 1980). Hazard (1977) observed that major hauling grounds in Tenakee Inlet, Alaska, are protected from wind and wave action, have moderate to steep slopes into water sufficiently deep for seals to swim, and are isolated from forested land by at least 200 m of open land or water. In Humbolt County, California, hauling grounds with sloping profiles or areas exposed by low tides are used more frequently than those with steep vertical sides that impede landing success. Pups are found principally at haulout areas where shallow water is easily accessible (Sullivan 1980). Man-made objects such as log booms, barges, and oyster floats sometimes are used as haulout sites by seals in Puget Sound, Washington (Calambokidis *et al.* 1978).

The slope of primary haulout areas varies among localities, apparently in relation to the magnitude of the tidal flux (Hazard 1977). For example, in southeastern Alaska where there is a tidal range of 7.5 m, seals haul out on shores with moderate to steep slopes (13°-47°) at least 4 m above low water (Hazard 1977). In areas with less extreme tides, seals are able to use more gently sloping shores and remain close to the water's edge (Sullivan 1980).

The time of hauling out is as varied as habitats used. The reported environmental factors associated with daily peak abundance of seals in various parts of the North Pacific region are summarized in Table 1. As the methods and provided information differ between studies, direct comparisons can not be made, but some trends are apparent. The kinds of substrates available, together with diel activity patterns, account for most of the variation observed among haul-out patterns. Tidal influences are greatest on gently sloping substrates (such as tidal flats), where minor tidal changes affect large surface areas. Weather may influence haul-out activity directly by its physical impact on the seals (e.g., heavy rain, high winds), as well as by secondary effects (e.g., heavy surf) on the haulout sites. For most terrestrial substrates, seals haul out in greatest abundance during ebbing and low tides, and in the absence of heavy rains, high winds, and intense disturbance. Noteworthy exceptions to this pattern have been seen in Puget Sound, where some marsh areas and logs were most easily accessible during high tides and where frequent daytime disturbances by man led to nighttime haul-out periods by the seals (Calambokidis _et al_. 1978). In areas where tide has little effect on substrate availability (e.g., on steep or broad beaches above high water, or on floating man-made objects), a diurnal schedule in haul-out activity is more apparent. There, peak numbers often are present early in the afternoon.

Unlike shoreline haulout sites which regularly are washed by

Table 1. Environmental parameters associated with peak abundance of harbor seals in the western North Pacific.

Habitat	Tide[1]	Time[2]	Weather[3]	Location	Reference
Tidal flats	L			SE Bering Sea, AK	Everitt and Braham 1980
	L			Skeena Estuary, BC	Fisher 1952
	L,F	A	F	Nanvak Bay, AK	Johnson 1976a
	L			Puget Sound, WA	Calambokidis et al. 1978
	L			Humbolt Bay, CA	Knudtson 1974
	L,F			Humbolt Co., CA	Sullivan 1980
	L	A	F[4]	Bolinas, CA	Allen 1980
Sand and cobble beaches	L,F	A	F	Tugidak Is., AK	Bishop 1967, Johnson 1976b
	All[5]			Tenakee Inlet, AK	Hazard 1977
	L	M[6]		Otter Island, AK	Johnson 1976a
	All			Smith Island, WA	Calambokidis et al. 1978
	F			McMiken Is., WA	Calambokidis et al. 1978
	L	A		Ano Nuevo Is., CA	White, 1979
	All	A		Channel Is., CA	Stewart, 1981
Rocky Shores	L		F	Glacier Bay, AK	Streveler 1979
	L,F			Humbolt Co., CA	Sullivan 1980
	L	A		Ano Nuevo Is., CA	White 1979
	L			Puget Sound, WA	Calambokidis et al. 1978
	L	M[6]		Otter Island., AK	Johnson 1976a
	All[5]			Tenakee Inlet, AK	Hazard 1977
	H,F			De Horsey Is., BC	Fisher 1952
	L			SE Bering Sea, AK	Everitt and Braham 1980
Glacial ice	All	D	All	Glacier Bay, AK	Streveler 1979
	R		W	Aialik Bay, AK	Bishop 1967
Human-made		N		Puget Sound, WA	Calambokidis et al. 1978

1. Tides: High (H), Falling (F), Low (L), Rising (R), No pattern (All)
2. Time: Morning (M), Afternoon (A), Day (D), Night (N)
3. Weather: Fair (F) absence of strong winds, heavy rain or rough surf.
   All (A) all weather affected seals similarly.
   Onshore winds (W)
4. Delayed haul out during storms from accentuated tides. Heavy rain startled and dispersed seals
5. Presence or absence of seals not directly related to tides.
6. Low tide always in morning.

high tides and are unavailable to resting seals, floating glacial is accessible at all tidal stages. Perhaps for that reason, few individuals were seen on the rocky shorelines in Aialik and Harris Bays (Bishop 1967), and in Glacier Bay (Streveler 1979); in those areas, the seals generally used only the ice. Streveler (1979) attributed annual fluctuations in the abundance of seals to the amount of ice discharged from the glaciers and the rapidity with which it was flushed from the inlets. He felt that the seals were attracted to glacial fjords only when the concentration of ice exceeded some lower limit, and that the seals shifted from one fjord to another if the concentration was below the minimum. Streveler (1979) judged that 87-99% of the seals which hauled out on the ice of Muir and Johns Hopkins Inlets, did so regardless of tide or weather. Conversely, the seals using haulout sites on the nearby Beardslee Islands and on the shores of Hugh Miller Inlet hauled out principally during sunny weather and at low tides. Bishop (1967) felt that tide and wind did exert an indirect influence on the seals' haul-out pattern by affecting the distribution of floating ice. Incoming tides and onshore winds tended to push the ice into Aialik Bay, compressing and stabilizing the seals' haulout area to within 4 km of the glacier; receding tides and offshore winds tended to disperse the ice. Dispersal of the ice resulted in dispersal of the seals, and an apparent decrease in the number of seals hauled out.

Use of haulout areas in winter is not well documented.

Observations by Johnson and Jefferies (1977), Mate (1977), Streveler (1979), Sullivan (1980), Francher (1981), Greybill (1981), Stewart (1981), and others indicate that the seals haul out less often in the winter than in summer. The seals appear to be dispersed along the coastline singly or in small groups; large herds of 50 - 100 have been seen infrequently (Streveler 1979, Dahl 1980).

Life-History

The birth of harbor seals typically takes place on shore or on ice; births in the water are uncommon (Johnson 1976a, Bishop 1967). Pups are highly precocial; they are born with their eyes open and with adult-type pelage, and they are immediately able to crawl and swim although in an uncoordinated manner (Knudtson 1974, Johnson 1976a). Often, they enter the water for the first time within an hour of birth. From the time of birth until weaning, the mother and pup seldom are apart (Knudtson 1974, Johnson 1976a). The duration of the nursing period is variable, ranging from 3 to 6 weeks (Bishop 1967, Bigg 1969a, Knudtson 1974, Johnson 1976a). Suckling usually takes place while the mother and pup are hauled out; occasionally it takes place in the water (Venables and Venables 1955, Bishop 1967, Knudtson 1974, Johnson 1976a). Weaning appears to be gradual. During the last week of the nursing period, either the mother or the pup may initiate temporary separations (Venables and Venables 1955, Johnson 1974, 1976a, White 1979) The mother increasingly rejects the pup's attempt at nursing and exhibits growing disinterest in the pup's presence (Lawson 1981). After the maternal bond is terminated, pups appear to disperse from their natal area (Johnson 1974, 1976a, Knudtson 1974).

Adult females ovulate between the end of lactation and 2 weeks after weaning the pup (Fisher 1954, Bishop 1967, Bigg 1969a). The breeding behavior is poorly understood. Aquatic displays associated with reproductive behavior have been described by many researchers (e.g., Venables and Venables 1957, Bishop 1967, Knudtson 1974, Johnson 1974, 1976a,b). Sullivan (1981) compared the displays exhibited between males with those between males and females. He concluded that mating was non-random and that dominance relationships between males determined breeding privileges. Splashing and "lobtailing" by males appear to function as both visual and acoustic displays, attracting the attention of estrous females and serving to warn other males. Soon after fertilization, further development of the embryo ceases, and the blastocyst remains dormant in the uterus. During this period of delayed implantation, the adult molts. Implantation of the blastocyst and development of the embryo resumes 1.5 to 3 months after fertilization (Fisher 1954, Harrison 1960, Bishop 1967, Bigg 1969a, Pitcher and Calkins 1979).

The molt of harbor seals takes place during a 6- to 8-week period, from the initiation of follicular activity until emergence of the new hair (Ling 1970). The seals spend more time hauled out during the molt than at other times (Johnson 1976a, Johnson and

Johnson 1979), apparently to enhance pelage growth by warming the skin (Feltz and Fay 1966). In addition, the seals' metabolic rate decreases during the molt, allowing them to spend less time feeding (Ashwell-Erickson and Elsner 1981). In the Gulf of Alaska, molting seals are seen from the beginning of June to early October, with a peak in occurrence in late July to early August (Pitcher and Calkins 1979).

Harbor seals generally are considered to be sedentary. Regional differences in pelage color, body size, and pupping times (Bigg 1969b, Shaughnessy and Fay 1977, Calambokidis et al. 1978, Pitcher and Calkins 1979, Bigg 1981, Kelly 1981, Burns and Gol'tsev in press) suggest that movements are minimal between large geographic areas. Nevertheless, radio tagging studies suggest that movements within those areas may be extensive (Pitcher and Calkins 1979, Beach and Jeffries 1981, Brown and Harvey 1981). Movements of radio-tagged seals of up to 194 km have been recorded (Pitcher and Calkins 1979). In western Alaska, large numbers of harbor seals enter the Kuskokwim estuary in summer but are absent in other seasons (F. H. Fay pers. comm.). Large numbers of non-breeding seals also move into nearby Nanvak Bay in late summer and move out again in autumn, before the bay freezes (Johnson 1975, 1976a). The harbor seals occurring in Kuskokwim and Nanvak Bays presumably spend the winter south of the pack ice in southern Bristol Bay, in which case they migrate 200 to more than 1,000 km per year. Radio-tracking studies conducted by Pitcher and Calkins (1979) on Tugidak

Island suggest that Tugidak is used as a full-time residence by some seals; other seals use it as a temporary haulout site, while en route to other localities.

Feeding Habits

Harbor seals feed on a diverse array of sublittoral and benthic prey in estuarine and marine waters. In the eastern North Pacific, the kinds of prey eaten by harbor seals show regional and seasonal variation (Scheffer and Sperry 1931, Imler and Sarber 1947, Fisher 1952, Wilke 1957, Spalding 1964, Kenyon 1965, Bishop 1967, Pitcher 1977, Calambokidis *et al*. 1978, Lowry *et al*. 1979, Pitcher and Calkins 1979). Major prey of Alaskan harbor seals include fishes of the families Gadidae, Clupeidae, Cottidae, Pleuronectidae, Salmonidae, Osmeridae, Hexagrammidae, and Trichodontidae, as well as octopus and gonatid squids. Decapods, primarily shrimps, may be important locally (Imler and Sarber 1947, Wilke 1957, Pitcher 1977, Lowry *et al*. 1979, Pitcher and Calkins 1979).

In the Gulf of Alaska, harbor seals show regional and seasonal variation in types of prey consumed (Pitcher 1977, Pitcher and Calkins 1979). In the eastern Gulf, walleye pollock (*Theragra chalcogramma*) are the dominant prey; in the western Gulf, octopus are dominant. Pitcher (1977) found seals in the Copper River Delta feeding primarily on eulachon (*Thaleicthys pacificus*), which move into the Copper River in spring and are gone by late summer.

Elsewhere in Prince William Sound, seals feed primarily on pollock in fall and winter, herring (*Clupea harengus*) in winter and spring, and salmon (*Oncorhynchus* spp.) in the summer; near Kodiak Island, seals rely mostly on capelin (*Mallotus villosus*) in the summer, Pacific sand lance (*Ammodytes hexapterus*) in the fall, and octopus in the winter (Pitcher and Calkins 1979).

Pups appear to feed mainly on crustaceans and small fishes after they have been weaned. Bigg (1973) reviewed the literature on prey consumed by newly weaned pups in both the Pacific and the Atlantic. He concluded that, for the first few weeks after weaning, pups feed mainly on the shrimp *Crangon*, before changing to a fish diet. Table 2 summarizes the more recent findings concerning prey eaten by pups in the North Pacific region. The results are similar. Invertebrates (shrimps and mysiids) were consumed by young pups up to 2 months of age, whereas older pups ate fishes. Fishes consumed by pups less than a year of age were smaller than those eaten by adults, being less than 130 mm in length (Pitcher and Calkins 1979). In the Gulf of Alaska, Pitcher and Calkins (1979) found pups feeding primarily on capelin and small pollock, with the proportion of capelin much higher (37.5%) than for older seals (9.2%).

Table 2. Prey of harbor seal pups in Alaska

		Pups	
Location	Prey	No.	Age
Gulf of Alaska[1]	Walleye pollock	2	4 Months
		1	5 Months
		2	Unspecified
	Capelin	5	10 Months
	Pacific tomcod	1	2 Months
	Pacific sandlance	1	Unspecified
	Unidentified fish	1	Unspecified
	Shrimps	1	2 Months
Aialik Bay[2]	Unidentified fish	1	Unspecified "Fat pup"
	Shrimp	1	Unspecified "Very thin pup"
Aleutian Islands[3]	Mysiids	3	"Recently weaned"

1. Pitcher (1977); Pitcher and Calkins (1979)
2. Bishop (1967)
3. Burns and Gol'tsev (in press)

STUDY AREA

Aialik Bay is a glacial fjord located on the southeastern coast of the Kenai Peninsula, southcentral Alaska (Fig. 1). Three major glaciers flow into the bay from the Harding Icefield: Holgate, Pederson, and Aialik (Fig. 2). Holgate and Aialik Glaciers discharge ice directly into the bay, whereas Pederson Glacier deposits its ice into a shallow lake. A few small pieces of ice from Pederson Glacier are carried downstream into Pederson Lagoon, and some eventually make their way into Aialik Bay. The study reported here was conducted principally at the base of Aialik Glacier.

The topography and vegetative cover of the shore of Aialik Bay is similar to that of the rest of the eastern Kenai Peninsula, with steep slopes characterized by stands of Sitka spruce (*Picea sitchensis*), thickets of alder (*Alnus crispa*), and small meadows on the lower slopes; the higher slopes are sparsely vegetated talus and bare rock. The shore of the bay is principally cobble beaches, interspersed with steep, rocky cliffs. Estuarine and freshwater habitats are present near Pederson Glacier. An approximately 5-m-deep sill (underwater glacial moraine) connects the northern ends of Pederson Spit and Coleman Bay. The sill is very steep and the basin north of it reaches a maximum depth of 190 m. Two major islands, Slate Island (approximately 2,000 m long) and Squab Island (approximately 300 m long), are situated north of the sill. Both islands are steep sided, with moderately sloping rocky shelves which

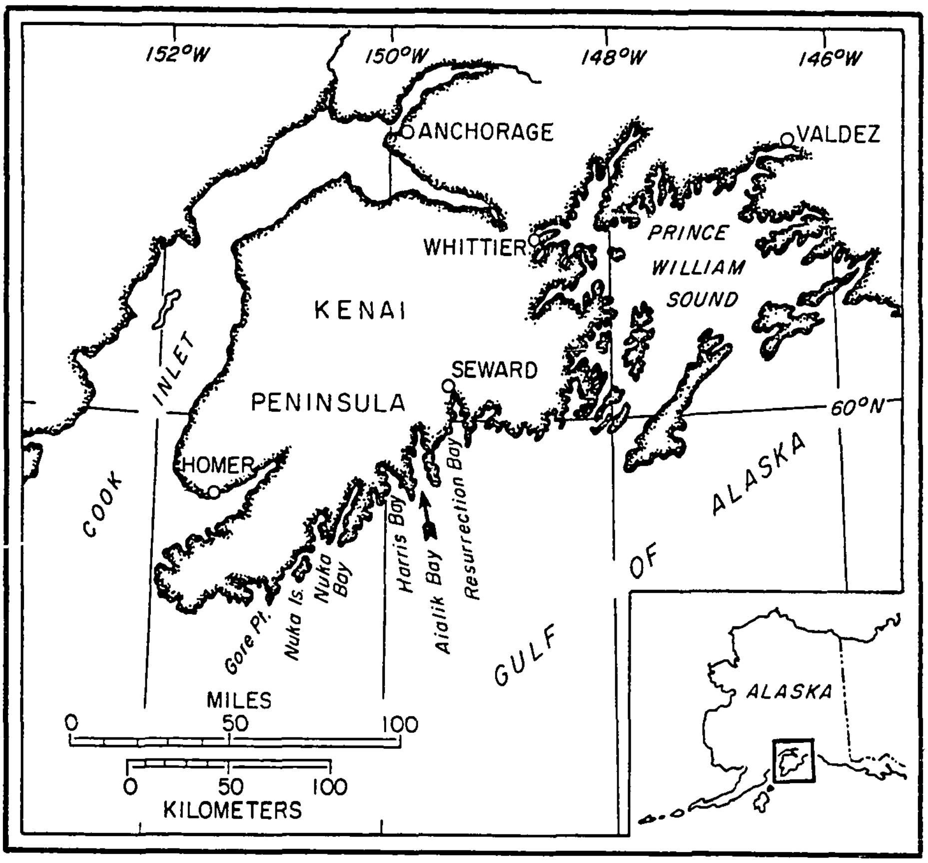

Fig. 1. Southern part of the Kenai Peninsula.

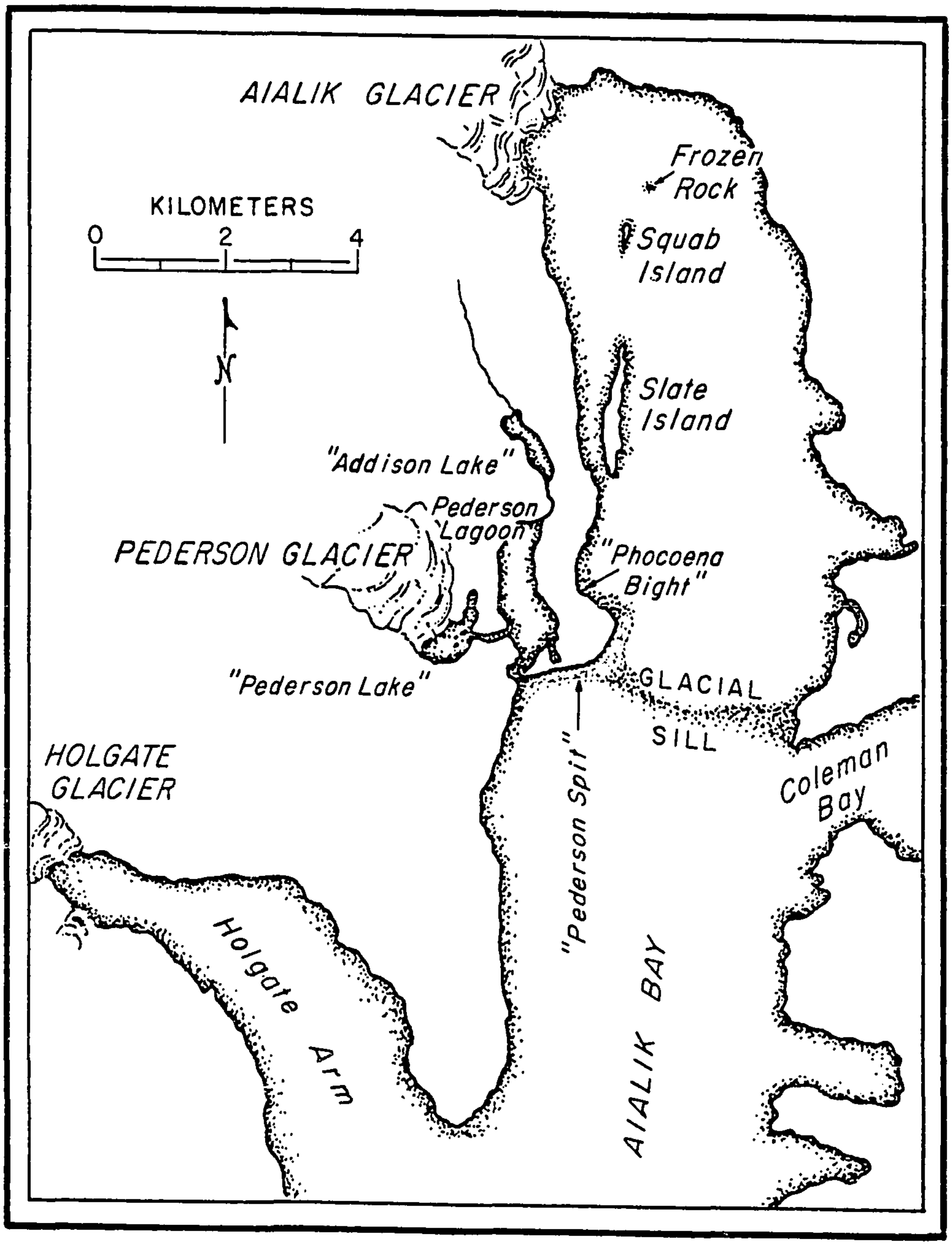

Fig. 2. Map of upper Aialik Bay

could be used by the seals as haulout sites at nearly all tidal levels. Frozen Rock, located north and east of Squab Island, is an unvegetated outcrop, exposed only during mid- and low-tides, when it is used occasionally by resting harbor seals and gulls. The shores of the upper bay often are washed by surf created by ice falling from the glacier. A southerly swell from the Gulf of Alaska occasionally washes the shoreline, especially during storms. Breaking waves generally are less than 1 m high but ocassionally reaches 12 m near the glacier. The tidal range in Aialik Bay is 5 m.

Glacial ice calved from Aialik Glacier is the primary substrate onto which harbor seals haul out in the upper bay. Its availability to the seals can be described on the basis of: (1) its distribution within the bay, (2) its composition in terms of size of bergs, and (3) the degree to which it is compacted. During this study, ice calved from the glacier ranged from a few millimeters to more than 25 m in diameter at the water's surface. From the glacier, the ice typically streamed southeastward, as it was carried by surface currents and pushed by the prevailing northwesterly breezes. Although it sometimes drifted down the length of Aialik Bay, the ice usually was confined north of the sill. Complex, northward movements of ice took place less frequently.

Almost always, the ice was clumped in large rafts. The rafts varied in size and compaction. Some were tightly packed, with no open water between bergs; others were more loose, with some amounts of open water between the bergs. The size of the bergs, their degree of compaction the size of the rafts depended on the amount of glacial activity, the direction and velocity of wind and surface currents, and the air and water temperatures. Typically, the ice was more abundant and widely distributed in early June, when glacial activity was high and water temperatures were low, than it was in August, when glacial activity was low and water temperatures higher.

METHODS

General Surveys

Between March 1979 and June 1981, I participated in four surveys of distribution and use of habitats by harbor seals along the eastern Kenai Peninsula and Prince William Sound. These included (1) an aerial survey by the Alaska Department of Fish and Game along the southeastern Kenai coast from 27 to 29 March 1979, (2) a shipboard survey conducted for the National Park Service via the _Shaman_ in southern Aialik Bay and in Harris Bay on 6 June 1979, (3) a shipboard survey aboard the R/V _Acona_ of Aialik Bay on 4 December 1979, and (4) a shipboard survey via the R/V _Alpha Helix_ in Aialik Bay on 3 December 1980.

The two winter surveys were done in conjunction with oceanographic studies conducted by C. P. McRoy, R. T. Cooney and T. C. Carpenter. Previous surveys of the abundance and distribution of harbor seals along the southern Kenai Peninsula from 1964-1978 (Bishop 1967, Bailey 1976, Pitcher and Calkins 1979) contributed further to the general understanding of harbor seal abundance and their distribution in Aialik Bay, relative to adjacent areas.

Aialik Bay Studies

I conducted field studies in upper Aialik Bay from 1979 through 1981. A base camp was maintained on Pederson Spit from 17 May to 17 August 1979 and was re-established the following year from

15 May to 23 August. A cabin south of Coleman Bay was used as a base camp from 21 May to 12 June 1981. From those locations, excursions were taken to Squab Island in a 4-m Zodiac boat powered by an outboard engine. Concurrent studies of marine productivity were conducted by T. C. Carpenter, University of Alaska, Fairbanks.

Censusing

I conducted censuses of the marine mammals at the head of Aialik Bay from the northern end of Squab Island with the aid of a Bushnell 25X spotting scope, a Bausch and Lomb 15-60X zoom spotting scope, and 7x35 binoculars. For this purpose, I subdivided the northern end of Aialik Bay into 32 areas, based on topographic features of the mainland shore and distance from Squab Island (Fig. 3 upper). The shoreline features were easily distinguishable with the unaided eye; the distance of the seals from the island was estimated with the aid of the 25X spotting scope as follows: in area 4, with Frozen rock at the lower edge of the field of view and the shoreline filling the top one-fourth, areas "B" and "C" were separated at the midpoint of the field (Fig. 3 lower). Subsection "A" was the area between Squab Island and Frozen Rock. The parts A, B, and C of the other sectors were then determined by rotating the scope on its tripod without changing its vertical angle. The shoreline, generally included in subsection C, ranged from 1.2 km to 3.5 km from my observation site on the northern end of Squab Island. Area A included water between 0-0.8 km from Squab Island, subsection B from 0.8-1.5 km, and subsection C from 1.5-3.5 km. Seals seen

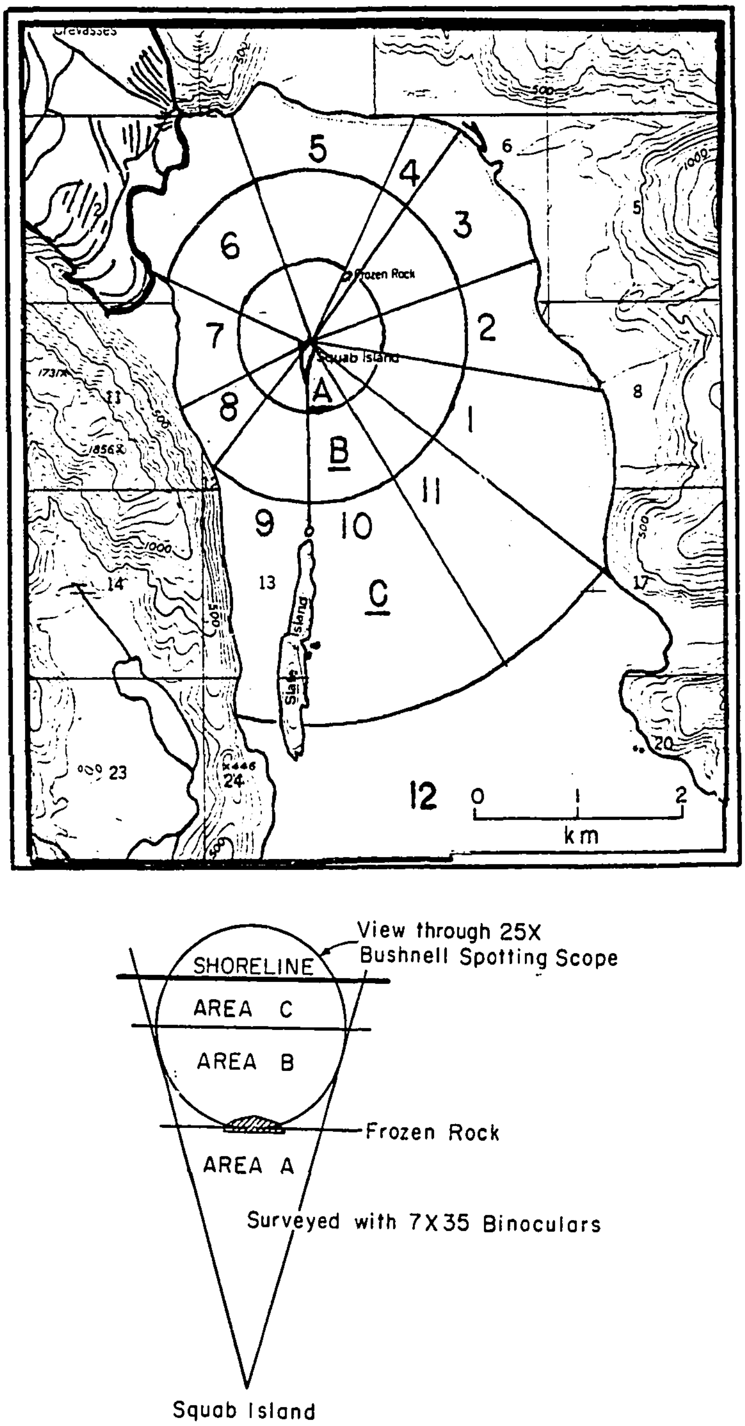

Fig. 3. Harbor seal study area in upper Aialik Bay.

beyond subsection C were included in area "12". Because the radial boundaries of the sectors were determined from distinctive topographic features on shore, the sectors were not of equal size

At each census, I recorded the date, time, tide, cloud cover, wind direction, wind velocity, precipitation, ice density, and direction of ice movement. I counted the total number of marine mammals observed on the ice and in the water, classifying the seals as adult female with pup, weaned pup, lone pup, or "other" (seals not conforming to those three categories). I also recorded all evidences of parturition and mortality. When viewing opportunities were optimal, I distinguished adult from subadult seals according to their relative size and shape (see below). Near the shoreline of subsections 1, 2, and 3 and in subsections 10c, 11c, and 12, I often was unable to discriminate pups and distinguish between adults and subadults because of the great distances. I distinguished the age composition of seals in those areas only under the best of viewing conditions. The numbers of pups recorded were conservative, since I often could not distinguish them in the most distant areas because of optical distortion by "heat waves". In all areas, they often were hidden behind other seals. I recorded the sex of seals only when I could see the individual's urogenital opening clearly.

In 1979, 1980, and 1981, I conducted a total of 134, 131, and 37 censuses, respectively. The time required for a census ranged from 15 min to 2 h 54 min, depending on the distribution of ice, the number of seals, and the type of census. The stated time (Alaska

Daylight Saving Time) for a census refers to the time when it was begun. Insofar as possible, I conducted one census during the middle of the day, between 1130 hrs and 1330 hrs -- the period in which maximal numbers of seals usually were visible. Other censuses were taken throughout the day as opportunity permitted, to monitor seal abundance as a function of time, weather, tides, and ice conditions. Fog and heavy rain often precluded counts because of poor visibility. Counts also were abandoned at times when wind speeds exceeded 10 m/s (20 kts), because of instability of the tripod and spotting scope.

Abundance Rank

To analyze the effects of tides, ice, weather, and diel activity rhythm on the number of seals on the ice, all census counts in each 5-day period were ranked relative to the highest count during that period. The highest count was assigned a value of 10 and each lower count was assigned a proportional value, rounded to the nearest integer. Ranking within 5-day periods was done to minimize the effect of seasonal fluctuations in numbers of seals.

The precision of the abundance rank is dependent on how well the highest count in the 5-day period approximates the greatest number of seals available to haul out during that period. The precision of the rank is reduced when the seasonal fluctuation in numbers of seals is large and takes place over a short period of time. The loss of precision caused by ranking may result in overly conservative results.

Unless otherwise specified, when examining the effects of specific parameters on seal abundance, I stratified the censuses into three daily time periods based on the similarity among their abundance ranks: morning (0300-0859 h), midday (1100-1459 h), and evening (1700-2259 h). From 0900-1059 h and 1500-1659 h were not included in the analysis due to the intermediate distribution of their abundance ranks.

Weather

I kept daily weather records, including maximum/minimum temperatures, visibility, and precipitation at the base camp. In addition, I recorded percentage cloud cover, wind velocity, wind direction, precipitation, and visibility at Squab Island at each census. Since weather conditions often changed rapidly, I used only those recorded at the time the census began for analysis.

I classified weather as: "fair", in periods of direct sunlight and partial cloud cover (usually after a storm or during periods between storms), "overcast" in times of hazy sunlight and overcast skies (before, during and between storms), and "foul" during periods of precipitation and high velocity winds. During the worst of the foul weather, conditions were unfavorable for censusing; hence the sample of censuses taken in weather of that type is biased toward the least unfavorable of the foul periods. I also classified weather recorded at the midday census according to the number of days before or after a storm, whichever was least. I considered those days that preceded and followed storms by equal periods as having followed the storm.

Tides

I coded each census relative to tidal stage (Elliott 1978, 1979, 1980), in order to include information on the currents associated with rising and falling tides, as well as to provide an index of tidal height. I did this with a circular code, based on the number of hours from the nearest high tide. Codes ranged from 0-1200, where 0 and 1200 were high tides and 600 was low tide. Values between 0 and 600 corresponded to falling tides; values between 600 and 1200 corresponded to rising tides. Categories used in analyses included: high (1030-1200, 0000-0129), falling (0130-0429), low (0430-0729), and rising (0730-1029) tides.

Ice Classification

At each census, I mapped the distribution of ice and recorded the ice-types. Ice was classified as to both its coverage of the water surface and the size of the bergs. I expressed ice coverage in "oktas" (eighths). For example, an area of 50% ice cover would be "4-okta" ice. I classified individual bergs as "small" (up to 1 m in diameter), "medium" (from 1 to 7 m in diameter), and "large" (more than 7 m in diameter). Medium-sized bergs usually were flat above the surface of the water; large bergs often showed extensive, irregular relief above the waterline and generally were unstable, tending to break apart and/or roll over.

I estimated the proportion of water's surface covered by bergs of each size-class, whenever I determined ice coverage. This was expressed in a fractional form, with total oktas of ice cover as the "numerator" and the size composition of the bergs as a 3-digit "denominator". Each digit of the denominator, from left to right, represented the oktas of small, medium, and large bergs, respectively. In order to examine seasonal variation in ice cover during 1979, I used a planimeter to determine the area covered by 7- to 8-okta, 4- to 6-okta, and 1- to 3-okta ice for each midday census. Census maps used in 1979 were different from those used in 1980 and could not be directly compared.

Age Composition

I determined the relative age of seals from their size and shape. Harbor seals in the Gulf of Alaska increase rapidly in length for 4 to 5 years, then more slowly until 7 years of age, when growth in length virtually ceases at a mean standard length (nose to tail) of 1.56 m for males and 1.46 m for females (Pitcher and Calkins 1979). In this study, the total length of the largest seals was estimated as 1.70 m (1.56 m for head and body + 0.14 m for the length of the hindflippers beyond the tail). All seals within 10% of that length were considered to be "adults". Smaller animals were classified as "subadults".

In 1979 and 1980, I classified all seals accompanied by pups as "adults", irrespective of their size. In 1981, however, I distinguished the larger "adult"-sized and from the smaller "subadult"-sized seals with pups. Data collected by Pitcher and

Calkins (1979) indicate that approximately 40% of the females accompanied by pups would be classified as "subadults" on the basis of size. Nearly all of the mature males were large enough to be classified as "adults". Thus, practically all "adults" were reproductively mature, but the "subadult" age category included some reproductively mature and virtually all of the reproductively immature seals.

I classified pups on the basis of their shape and size as, (1) newborn to one week old, (2) dependent pups more than one week old, (3) weaned pups, and (4) age unknown. Pups up to one week old still were rather thin and often had part of the umbilicus still attached. Older dependent pups were appreciably fatter, having a more adult-like shape, and lacking any remnant of the umbilicus. Weaned pups were especially fat and were either hauled out alone, in mixed herds, or in the company of a fat seal not likely to be the mother.

Distances between seals and size of ice bergs were estimated in relation to the total length of adult seals.

Group Density

Seals were classified into six types of groups, on the basis of numbers and density (Fig. 4): single seals (type I), a few seals in loose aggregation (type II), moderately dense aggregations (types III and IV), and densely aggregated groups (types V and VI). Females with pups were treated as a single individual.

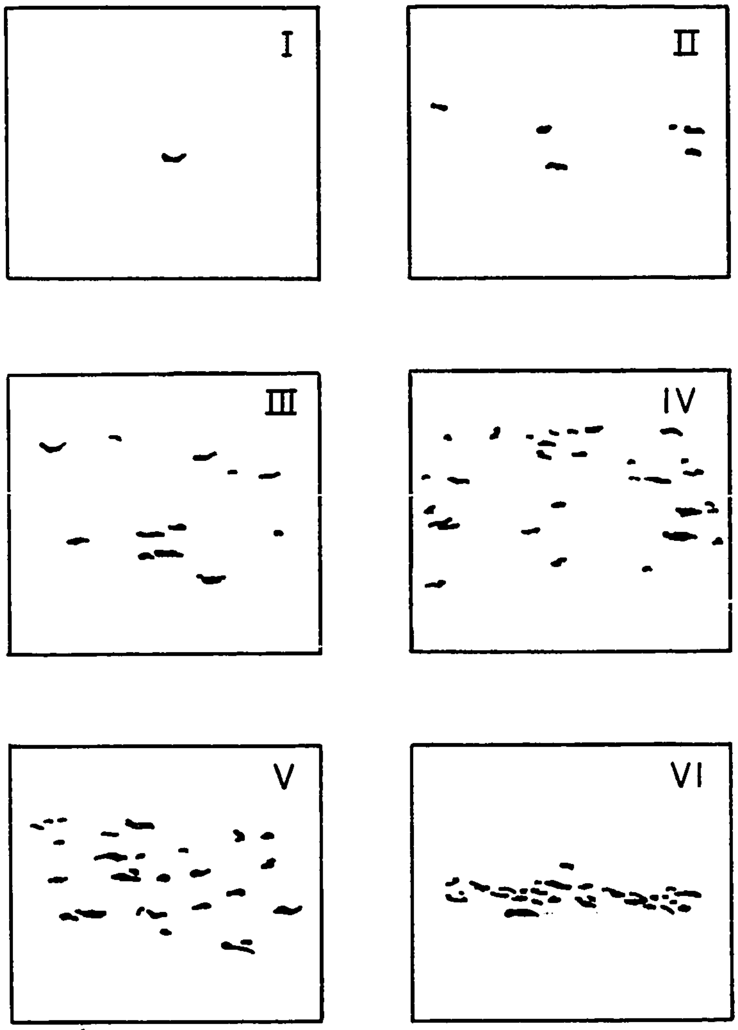

Fig. 4. Classification of groups of harbor seals on the basis of numbers and density.

Habitat Use

I examined the use of ice by harbor seals in three ways. First, seals, I assembled information on the size of bergs used, the distance to the nearest occupied berg, the group density, the ice conditions, and the age of all seals sharing a berg. Second, during censuses, I mapped and classified the location of seals according to group density and ice conditions, with notation of all females with pups sharing bergs with other seals and the age and sex of those seals. Third, since ice conditions appeared to influence the number of seals hauled out, I plotted ice maps at each midday census and, using a planimeter, calculated the area covered by 7- to 8-okta ice (the prefered ice cover). Due to the low viewing angle from Squab Island, the okta values may have been overestimated. Also, they may have been biased in favor of areas near Squab Island. For those reasons, the okta-values should be considered as ranks, rather than as absolute values.

Parturition

Sites of recent parturition were identified from large amounts of blood on the berg and the presence of a newborn pup or of scavenging birds. In each instance, I recorded the date, time of day, berg size, distance to nearest occupied berg, age class of nearest seal, number and species-composition of scavenging birds, and behavior of the female and her newborn. Although I saw births between census periods, I calculated parturition rates only on the basis of those sites observed during census periods, at which time the upper bay was surveyed entirely. Since parturition sites appeared fresh for up to two hours, calculated rates based on the duration of the census may overestimate the actual rate of parturition, bloody bergs seen during one census were monitored and were not re-counted in the next census.

Trawl Samples

To investigate the kinds of prey available to harbor seals in Aialik Bay in winter and summer, five otter trawl samples were taken north of the sill and east of Slate and Squab Islands (Table 3). Also, an Issac-Kidd mid-water trawl was used to sample organisms in the water column in Aialik Bay in winter.

Statistical Analysis

Statistical methods and analyses followed those of Conover (1971). The Biomedical Computer Program statistical package (Dixon 1981) facilitated multivariate analysis.

To examine interactive effects of environmental factors on seal abundance and on ice cover, I used a multiway frequency table analysis (Dixon 1981). For example, when considering the interactive effects of environmental variables on seal abundance, I constructed a four-way contingency table, grouping the data by tide, weather, time of day, and seal abundance. I then used the routine BMDP 4F (Dixon 1981) to test for significance of various interaction terms. This analysis tests the degree of departure of particular models from a saturated model which specifies all possible

Table 3. Epibenthic and mid-water trawls taken in Aialik Bay, 1979-1982

Date	Location	Time	Latitude/longitude	Bottom depth	Distance	Platform
OTTER TRAWLS						
4 December 1979	Aialik Bay	1504	59°54.7'N 149°42.4'W to 59°53.0'N 149°42.3'W	140 m	2.9 km	R/V Acona
11 June 1980	Aialik Bay	2030	59°56.1'N 149°41.9'W to 59°54.0'N 149°40.4'W	80-96 m	4.5 km	R/V Alpha Helix
3 December 1980	Aialik Bay	0540	59°53.1'N 149°41.5'W to 59°56.3'N 149°41.9'W	192 m	5.9 km	R/V Alpha Helix
3 December 1980	Aialik Bay	0710	59°56.3'N 149°49.9'W to 59°54.3'N 149°41.6'W	140 m	3.8 km	R/V Alpha Helix
11 June 1982	Aialik Bay*	--	----	---	---	R/V Alpha Helix
ISSAC-KIDD TRAWL						
3 December 1980	Aialik Bay	0315	59°53.1'N 149°41.5'W to 59°54.5'N 149°41.2'W to 59°53.0'N 149°41.5'W	180 m	5.4 km	R/V Alpha Helix

* Exact location and trawling methods are unknown.

interactions among the variables. The objective of this analysis is to find the simplest model that generates expected frequencies adequately fitting the observed frequencies.

The log-linear model (for mutual independence of the variables) is of the form:

$$\ln e_{\alpha,\beta,\phi,\delta} = u + u_{A(\alpha)} + u_{H(\beta)} + u_{T(\phi)} + u_{W(\delta)}$$

where e equals the expected frequency for a cell with parameter categories α,β,ϕ, and δ. A, H, T, and W refer to the parameters: seal abundance, time of day, tide stage, and weather, respectively. The variable "u" is the overall mean effect; u_A is the main effect of abundance; u_H is the main effect of time of day, and so forth. The main effects are defined in terms of deviations from the overall mean effect (see Whittam and Siegal-Causey 1981); likewise, interactions (e.g., u_{AH} measure deviations from the lower order parameters (e.g., $u_{A(\alpha)}$ and $u_{H(\beta)}$). In reporting the results, the log-linear model will be refered to by the subscripts of the parameter (e.g., $A = u_{A(\alpha)}$). The level of interactions are described in terms of their order; first order interactions are the effects of a single parameter such as A; second order interactions are the combined effects of two parameters such as AH; third order effects are that of three parameters such as AHW and so forth. Higher order interactions imply the inclusion of related lower order interactions. For instance, ATW includes the effects of ATW, AT, AW, TW, A, T, W.

The model sought is the simplest one which provides a reasonably close fit between the observed and expected values resulting in a non-significant ($P > 0.05$) departure from observed values.

RESULTS

Distribution and Movements

The primary location of resting harbor seals in Aialik Bay was on the floating ice near the foot of Aialik Glacier. The distribution of seals on the ice and the type of ice used varied with the amount and quality of ice available. On apparently homogeneous expanses of ice, the seals usually were not uniformly distributed but were clumped.

The amount of ice coverage affected the distribution of seals and the number that hauled out (Fisher exact test, $P = 0.027$, $n = 28$). During 60% of the midday censuses, the seals had an abundance rank of 10 when 7- to 8-okta ice covered at least 6% of the area north of Slate Island. When less ice was present (Fig. 5), only 12% of the midday censuses attained a rank of 10. During those periods of less ice, when few seals were on it, seals were numerous in the water throughout the upper bay, especially near the foot of the glacier. Those seals generally did not haul out unless the glacier calved enough new ice to form another 8-okta raft. In such instances, all apparently suitable bergs were occupied, often to the maximum.

Typically when seals were not on the ice, they swam throughout the bay, as well as into Pederson Lagoon and Addison Lake. From my intermittent observations at Pederson Spit, I gained the impression that most of the seals were swimming southward, out of Aialik Bay, in the evenings and northward, into upper Aialik Bay, in the

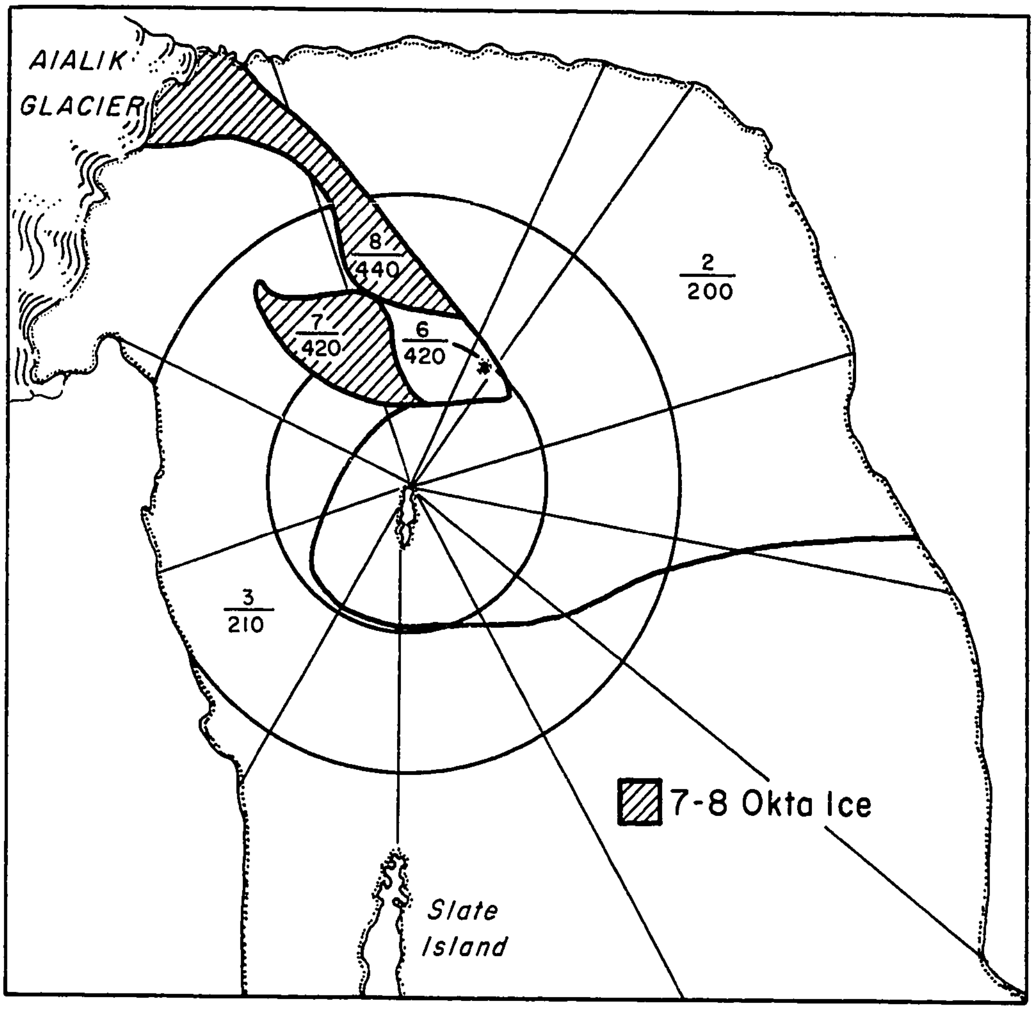

Fig. 5. Example of distribution of ice which limited the number of seals able to haul out in Aialik Bay on 23 May 1980.

mornings.

The results of my winter surveys, compared with the spring-summer census data, have indicated that seals rest on the ice less during in the winter than they do during the spring and summer. On 4 December 1979, I observed only nine seals hauled out in Aialik Bay. On 3 December 1980, 69 seals were observed in the upper bay, but only 22 of those were on the ice. Each of these censuses was conducted under optimal weather conditions at midday, and the ice was sufficient to accommodate much larger numbers than were present. Fred Woelkers (pers. comm.), a frequent visitor to Aialik and Harris Bays several years ago, stated that harbor seals occasionally haul out on the ice in winter in numbers approaching summer levels. Streveler (1979) observed that the number of seals throughout Glacier Bay during the winter was about 50% of the number seen during the spring and summer.

Haul-out Schedule

During the spring and summer, the number of seals resting on the ice in Aialik Bay varied from day to day and from month to month (Fig. 6). The greatest numbers of seals were present in early June and mid-August, during the pupping and molting periods, respectively; the least numbers were seen in May and July, before pupping began and during the breeding period. Fluctuations among days in the number of seals sighted on the ice varied with the time of day the census was taken, as well as with weather and ice conditions.

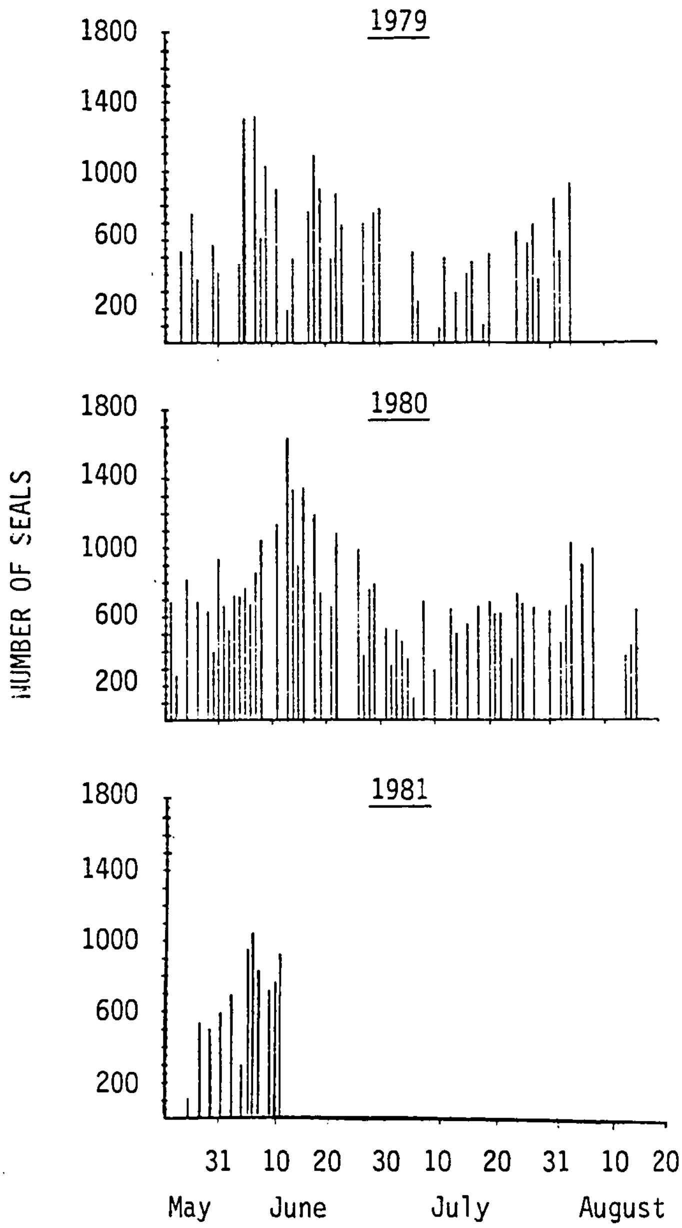

Fig. 6. Variation of daily maxima in censuses of harbor seals on the ice in upper Aialik Bay, spring and summer, 1979-1981.

Diel Activity Cycle

The numbers of seals hauled out on the ice in Aialik Bay showed strong diurnal cycles throughout the spring and summer. The greatest numbers of seals were seen on the ice from 1100 h to 1700 h; the least numbers were on the ice at night, between 1900 and 0700 h (Fig. 7). This diurnal variation was highly significant (Kruskal-Wallis test, $T = 75.68$, $df = 9$, $P < 0.001$). Seals were seen to haul out mostly during the morning, especially from 0700 to 1100 h. They also were seen to re-enter the water throughout the day, often abandoning the ice when it was unable to support them any longer or when they were disturbed by other seals, boats, aircraft, birds, or waves. The decline in numbers on the ice during the afternoon and evening (1500-2200 h) was attributable in part to deterioration (melting) of the ice, but even the seals on large, apparently stable bergs entered the water during that period. The diel cycle in use of the ice roughly coincided with variation in abundance of ice. Rafted ice generally was prevalent throughout the day and night in May and June but was most abundant in midday and least abundant at night in July and August (Fig. 8).

Influence of Weather

Weather influenced the number of seals on the ice, both by its direct impact on the seals and by indirect effects through dispersion of the ice. The distribution of abundance ranks for censuses taken during fair, overcast, and foul weather, in morning, midday, and evening is shown in Fig. 9. Foul weather tended to have

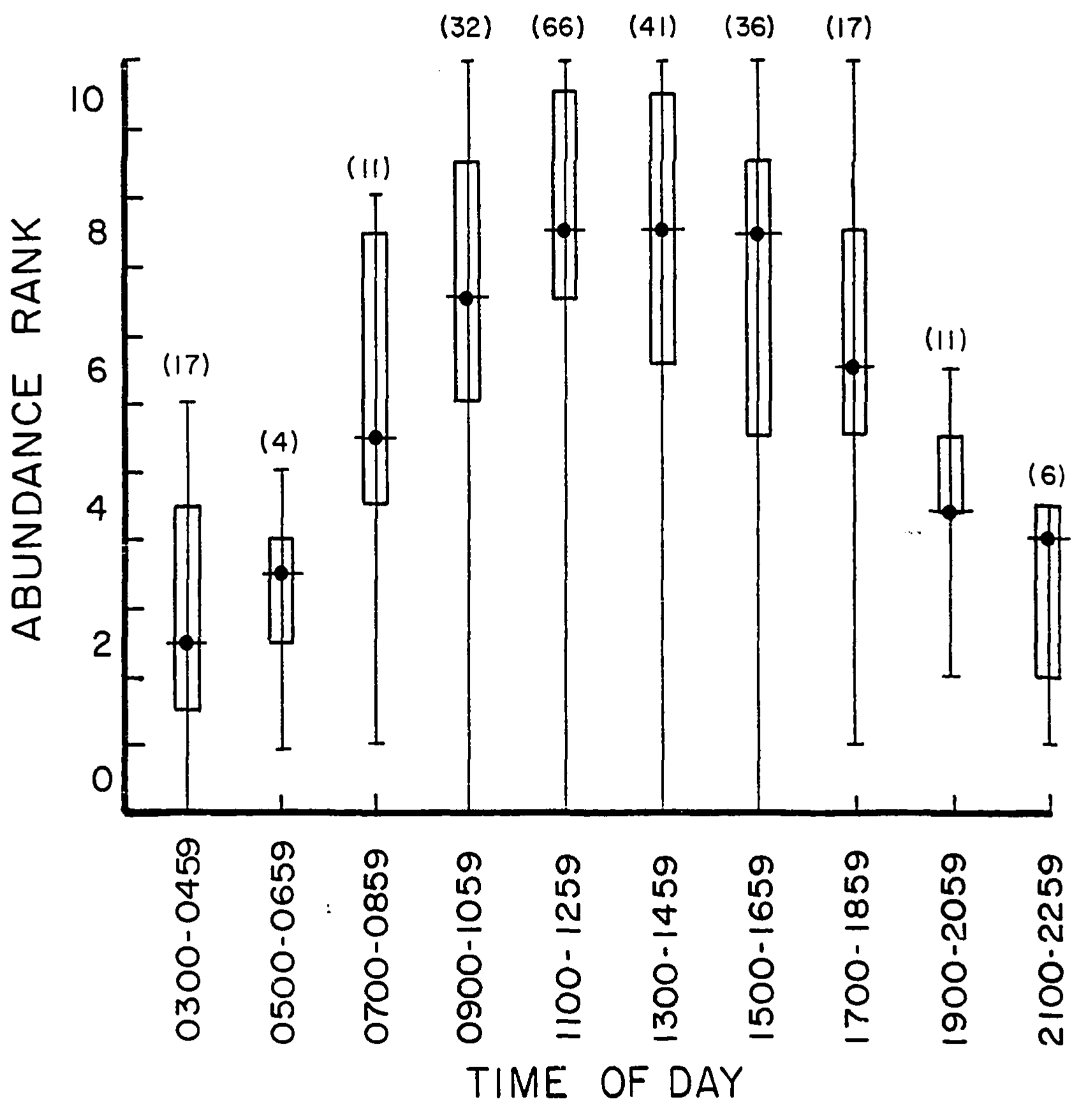

Fig. 7. Relationship between time of day and abundance of harbor seals on the ice in Aialik Bay, 1979-1981.

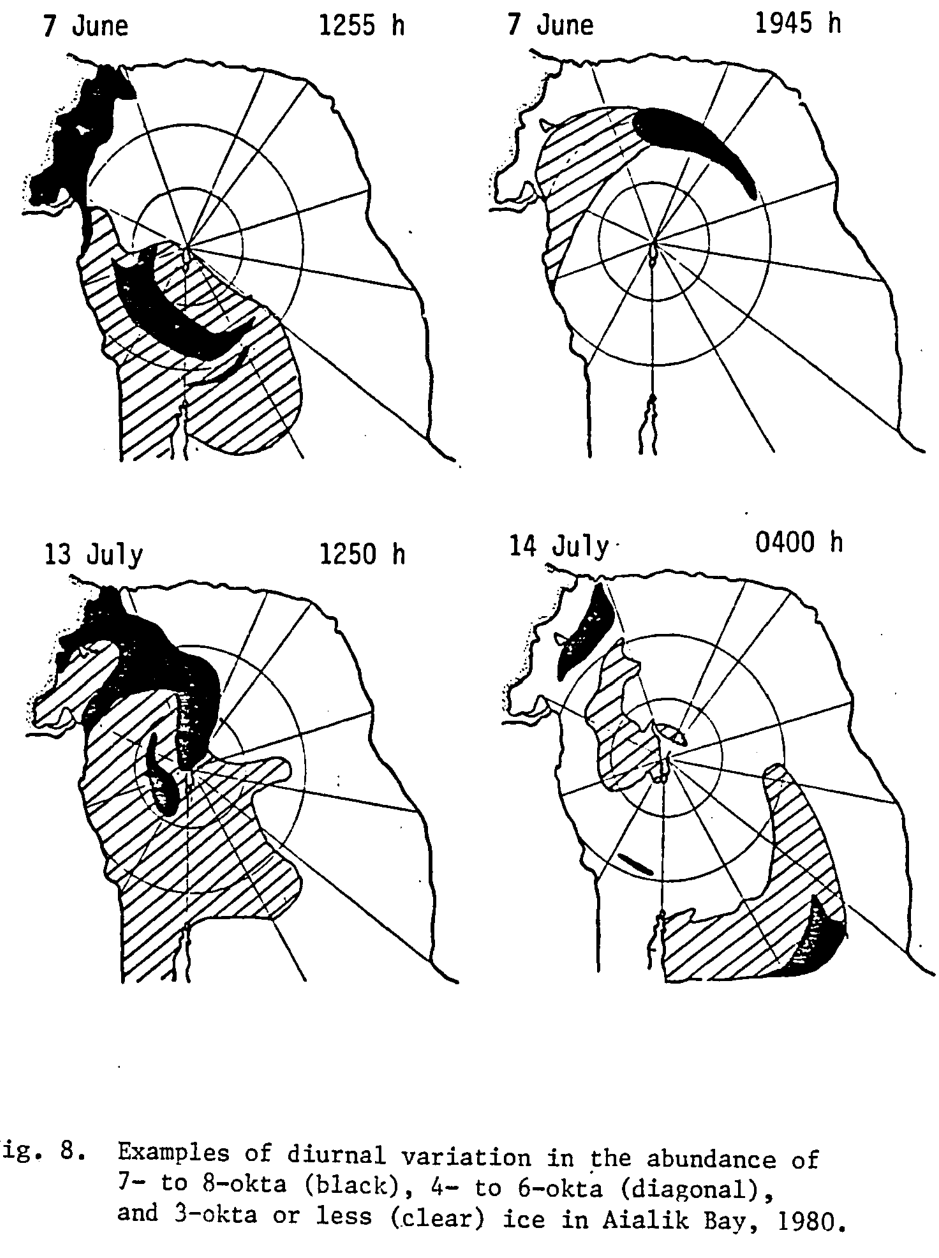

Fig. 8. Examples of diurnal variation in the abundance of 7- to 8-okta (black), 4- to 6-okta (diagonal), and 3-okta or less (clear) ice in Aialik Bay, 1980.

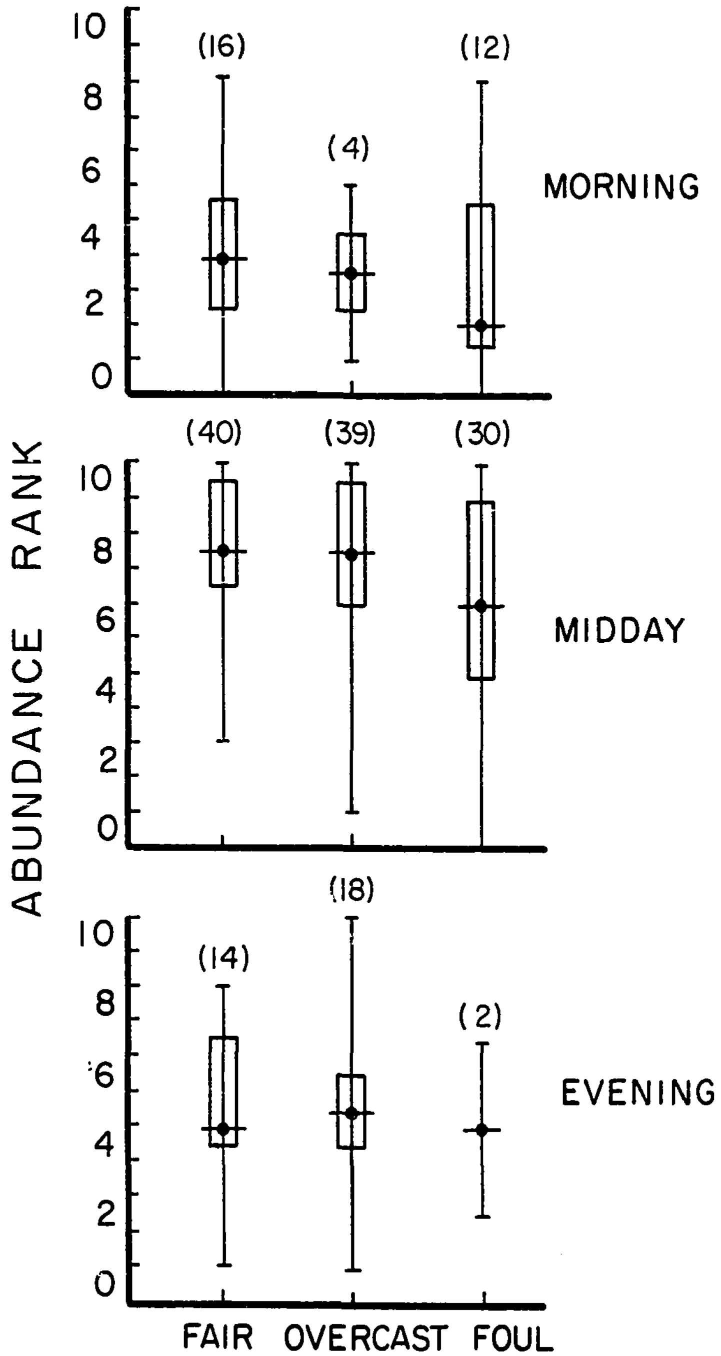

Fig. 9. Relationship between weather and harbor seal abundance on ice in Aialik Bay, 1979-1981.

a depressing effect on abundance, particularly in morning and midday; abundance ranks during fair and overcast weather were equally higher than those during foul weather. Differences between foul and fair-overcast conditions were significant (Kruskal-Wallis test: $T = 12.24$, $df = 2$, $P < 0.005$).

Seals appeared to anticipate the coming of a storm, for they tended not to haul out during the preceding day (Fig. 10). During the storm, the seals hauled out in moderate numbers, similar to those two or more days before the storm. Seals hauled out in greatest abundance for two days following the storm. These differences were highly significant (Kruskal-Wallis test: $T = 14.14$, $df = 5$, $P < 0.025$).

High velocity winds appeared to have the greatest effect on the number of seals on the ice (Fig. 11). During serial counts of seals on the ice at 2- to 4-h intervals over a 25-h period of increase and subsidence of wind velocity (from 1500 h on 26 May to 1600 h on 27 May 1979), the number of seals declined to about 10% of the expected values when winds increased to 10 m/s (20 kts). As wind velocity subsided, the number of seals on the ice again approached the expected values. Part of the decline in numbers may have been caused by the wind's dispersing the ice, blowing it southeastward. Typically, however, the seals rapidly abandoned the ice, even before it was appreciably dispersed, and they generally did not haul out again until the wind decreased greatly in velocity.

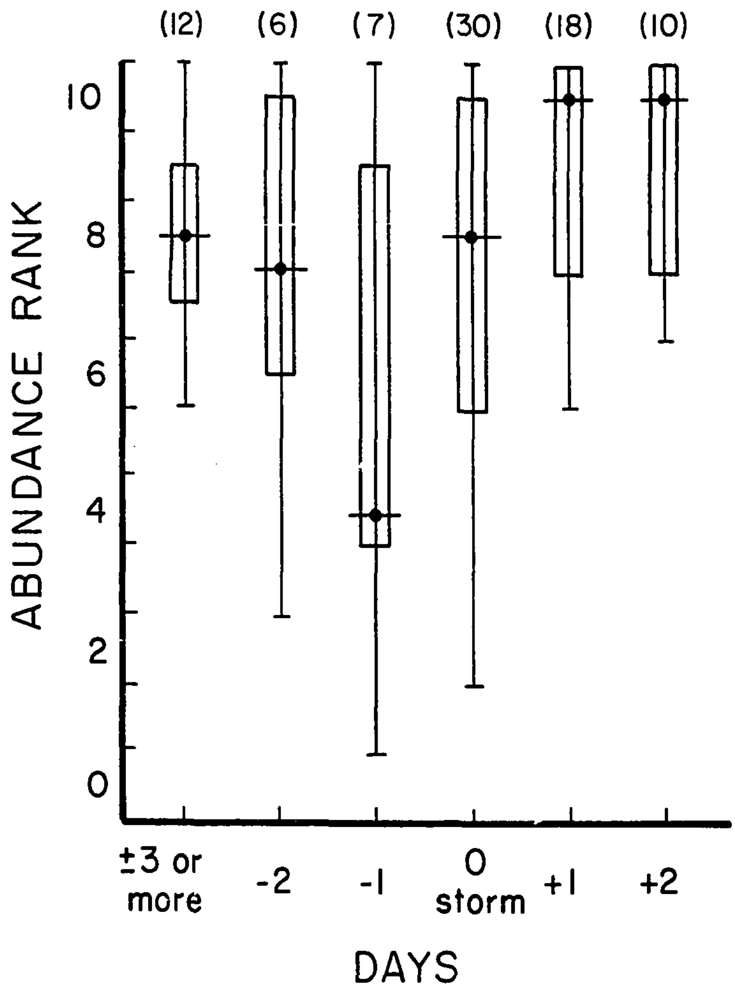

Fig. 10. Abundance of harbor seals hauled out in relation to storms in Aialik Bay, 1979-1981.

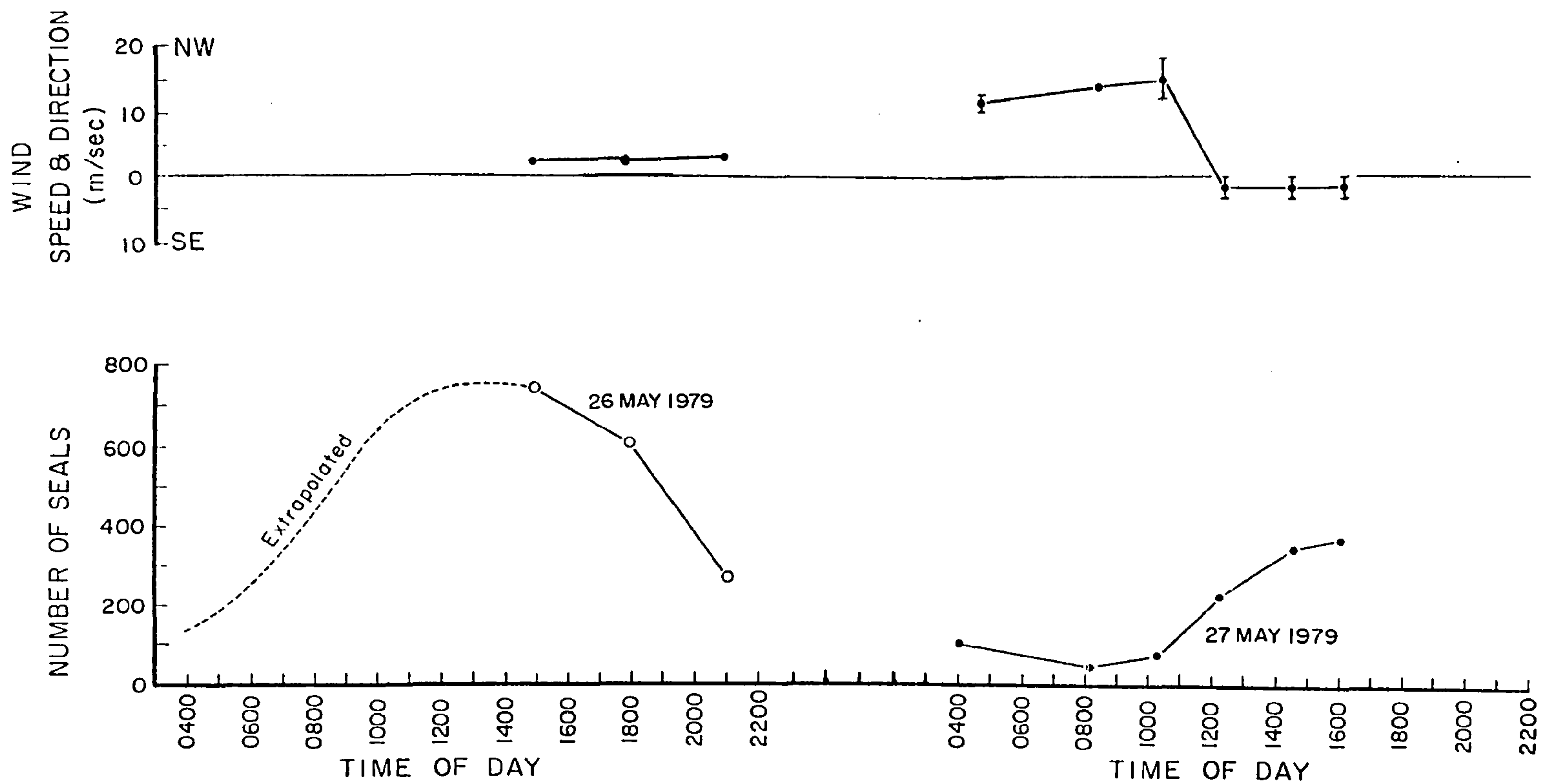

Fig. 11. An example of the effect of strong northwesterly winds on the number of harbor seals hauled out in Aialik Bay.

Tidal Influences and Dispersion of Ice

Tides and currents in Aialik Bay influence the distribution of the ice, but they do not affect the surface area of ice available to seals. Bishop (1967) believed that incoming tides and onshore winds tended to push the ice into the bay, compacting and stabilizing it within 2-4 km of the glacier. He felt that receding tides and offshore winds tended to disperse the ice. In his experience, fewer seals were hauled out on the dispersed ice than on compacted ice.

To test Bishop's impressions, I analyzed the relationship between direction and rate of ice movement and tidal stage using a multiway frequency table analysis (Dixon 1981). These parameters were not mutually independent. The model which included the single interactive effect between direction of ice movement and tidal stage (Table 4) was the only one which resulted in expected values which did not deviate significantly from the observed values (Table 4). Interactive effects including the rate of ice movement did not significantly inhance the model even though northward ice movements tended to be slower than southward movements.

I was unable to measure directly the effect of winds on ice movement. The direction and velocity of winds varied locally over the upper bay, and my measurements taken on Squab Island were not representative of conditions in other localities. Along the eastern part of the bay, there was often an opposing southerly "bay breeze" in the afternoon, and along the northern shore, especially near the glacier, the prevailing northwesterly breeze was much stronger than

Table 4. Direction and rate of ice movement relative to tidal stages in Aialik Bay, 1979-1981.

Tidal stage	Direction and rate of ice movement					
	Northward			Southward		
	N	Slow	Med-fast	N	Slow	Med-fast
Rising	8	75%	25%	33	45%	55%
High	17	59%	41%	22	41%	59%
Falling	2	100%	0%	26	23%	77%
Low	3	33%	67%	34	41%	59%
Total	30	63%	37%	115	38%	62%

Results of multi-way frequency table analysis.

Model [a]	G^2	df	P
Mutual independence			
R,D,T	27.75	10	0.002
One interactive effect			
RD,T	22.04	9	0.009
R,DT	11.31	7	0.126
RT,D	23.87	7	0.001

a. R = Rate of ice movement; D = Direction of ice movement; T = Tidal activity.

on Squab Island. Overall, strong northwesterly winds did move the ice southward, even against the rising tide; strong southerly breezes (5-10 kts) also were seen to push the ice northward during falling tides.

For an indirect test of the effects of winds on ice movement, I compared the relationship between direction of movement and tidal stage in the morning (0300-1259 h), when the northwesterly breeze prevailed with that in the afternoon and evening (1300-2259 h), when the "bay breeze" often blew in the southern and eastern parts of the bay (Table 5). A multi-way frequency table analysis (Dixon, 1981) again showed the interactive effect between tidal stage and time of day. Interactive effects associated with the time of day (i.e. wind direction) did not significantly improve the model. Hence, the southerly "bay breeze" does not appear to have the effect hypothesized by Bishop (1967).

I compared abundance ranks of harbor seals and tidal stages during three time periods (morning, midday, and evening); the relationships were weak in all periods (Fig 12). During the morning and evening, the number of seals on the ice showed little variation between tidal stages (Kruskal-Wallis test; morning: $T = 2.47$, $df = 3$, $P > 0.25$; evening: $T = 3.07$, $df = 3$, $P > 0.10$). Differences in seal abundance between tidal stages tended to be greatest (Kruskal-Wallis test, $T = 7.92$, $df = 3$, $P < 0.05$) at midday, when abundance ranks were higher during falling than other tides and significantly lower during low tides.

Table 5. Time of day and direction of ice movement relative to tidal stages in Aialik Bay, 1979-1981.

Tidal stage	Time of day[a] and direction of ice movement					
	Morning			Afternoon and evening		
	N	North	South	N	North	South
Rising	39	23%	77%	35	17%	83%
High	26	31%	69%	29	52%	48%
Falling	22	14%	86%	19	21%	79%
Low	27	4%	96%	18	11%	89%
Total	114	18%	82%	101	27%	73%

Results of multi-way frequency table analysis.

Model[b]	G^2	df	P
Mutual independence			
H,D,T	25.29	10	0.0048
One interactive effect			
HD,T	23.16	9	0.0059
H,DT	5.86	7	0.5563
HT,D	23.66	7	0.0013

a. Morning is before 1300 h; Afternoon and evening is 1300 h and later.
b. H = Time of day; D = Direction of ice movement; T = Tidal activity.

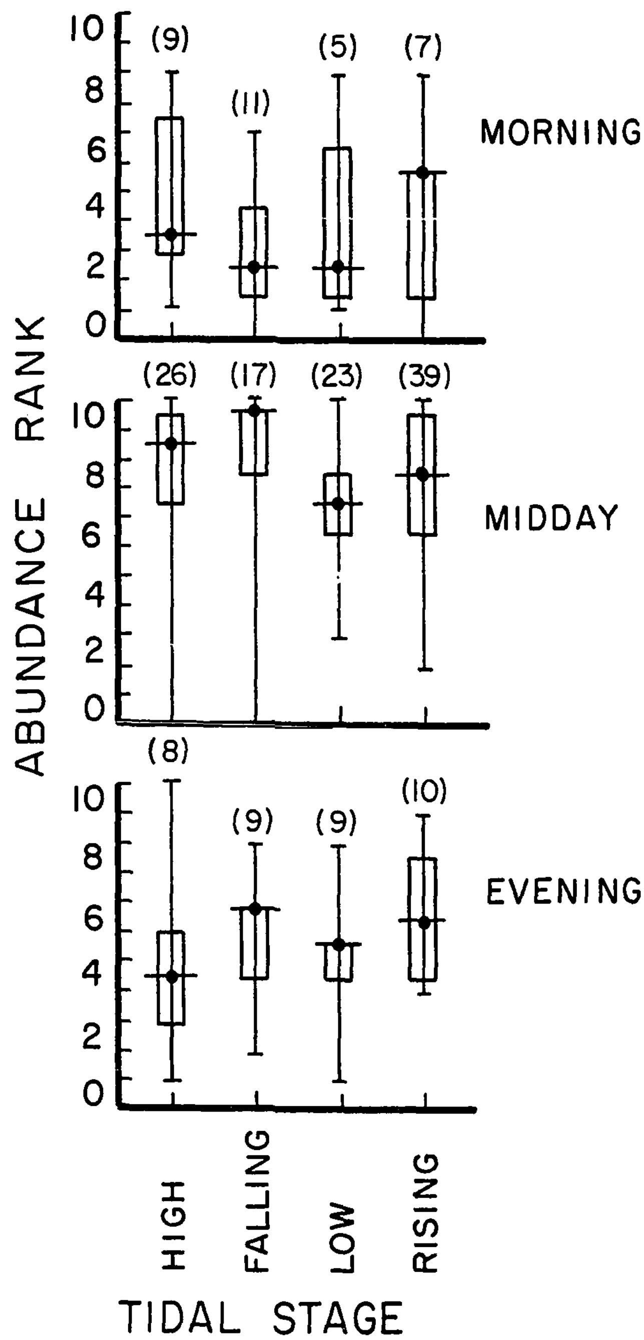

Fig. 12. Relationship between tidal stage and harbor seal abundance in Aialik Bay, 1979-1981.

Multivariate Analysis

Multivariate analysis of seal abundance in relation to tides, weather, and time of day was used to examine the interactive effects of those environmental variables on the seals, as well as to describe the relative strengths of their relationships. A contingency table (Table 6) was constructed for this purpose and tested by means of a log-linear model, multiway frequency table analysis (BMDP 4F; Dixon 1981). Screening of data showed that interactions between abundance and time of day (AH), abundance and weather (AW), and abundance and tidal stage (AT) contributed to the prediction of observed values sufficiently for consideration for the log-linear model; contributions from third and fourth order interactions were not sufficient. Five models were constructed to test for causes of variation in the number of seals seen (Table 7).

To test the hypothesis of independent assortment of the four variables (T,W,H,A), I used the model for mutual independence (Table 7) to generate expected frequencies. I rejected this hypothesis because the expected values did not fit the observed values well ($G^2 = 66.54$, df = 18, $P < 0.001$). The simplest model that fits the observed data reasonably well was: A,H,T,W,AH ($G^2 = 19.01$, df = 16, $P > 0.27$). The interaction between abundance and time of day had a probability greater than 0.05, and it generated expected values that did not significantly deviate from the observed values. To test whether any additional parameters significantly decreased the likelihood of goodness of fit, the

Table 6. Contingency table used for multiway frequency table analysis of the relationship between seal abundance, time of day, weather, and tidal stages in Aialik Bay, 1979-1981.

Weather	Tide	Time	Abundance rank			N
			0-4	5-7	8-10	
Overcast-fair	High-rising	1700-0900	13	8	4	25
		1100-1500	3	13	28	44
	Low-falling	1700-0900	15	9	3	27
		1100-1500	2	8	21	31
Foul	High-rising	1700-0900	4	1	2	7
		1100-1500	5	8	9	22
	Low-falling	1700-0900	6	1	0	7
		1100-1500	2	4	2	8

Table 7. Summary of results from the multiway frequency table analysis of the relationship between seal abundance, time of day, weather, and tidal stages in Aialik Bay, 1979-1981.

Model[a]	G^2	df	P
Mutual independence			
A,H,T,W	66.54	18	0.00
One interactive effect			
A,H,T,W,AH	19.01	16	0.27
A,H,T,W,AW	63.11	16	0.00
A,H,T,W,AT	64.82	16	0.00
Two interactive effects			
A,H,T,W,AH,AW	15.58	14	0.34
A,H,T,W,AH,AT	17.29	14	0.24
Three interactive effects			
A,H,T,W,AH,AT,AW	13.87	12	0.31

a. H = time of day; A = abundance; T = tide; W = weather differences between G^2 values for models with presence or absence of each parameter were calculated; degrees of freedom were derived from the difference between the degrees of freedom for each model. More complex models failed to find additional interactions which significantly decreased the test statistic. The model which best predicted the observed frequencies was:

$$\ln e_{\alpha,\beta,\phi,\delta} = u + u_{A(\alpha)} + u_{H(\beta)} + u_{T(\phi)} + u_{W(\delta)} + u_{AH(\alpha\beta)}$$

The conclusion from this is that the abundance of seals resting on the ice, although affected by weather and tides (as noted previously), was overwhelmingly influenced by the diel activity rhythm of the seals.

Population, Life Cycle and Social Behavior

Age Composition

The age composition of the harbor seal population inhabiting the ice in upper Aialik Bay varied throughout the summer of 1979, 1980, and 1981 in both relative (Fig. 13) and absolute (Fig. 14) numbers. In May of each year, about 600-800 seals were present; about 65% of those were subadults (including small pregnant females). During the peak of parturition (4-7 June) and for a short time thereafter, adults predominated while subadults were declining in numbers. By mid-June, well after most pups were born, the number of seals on the ice had increased to about 1,300 to 1,600 individuals; at the same time, the proportion of adults had risen

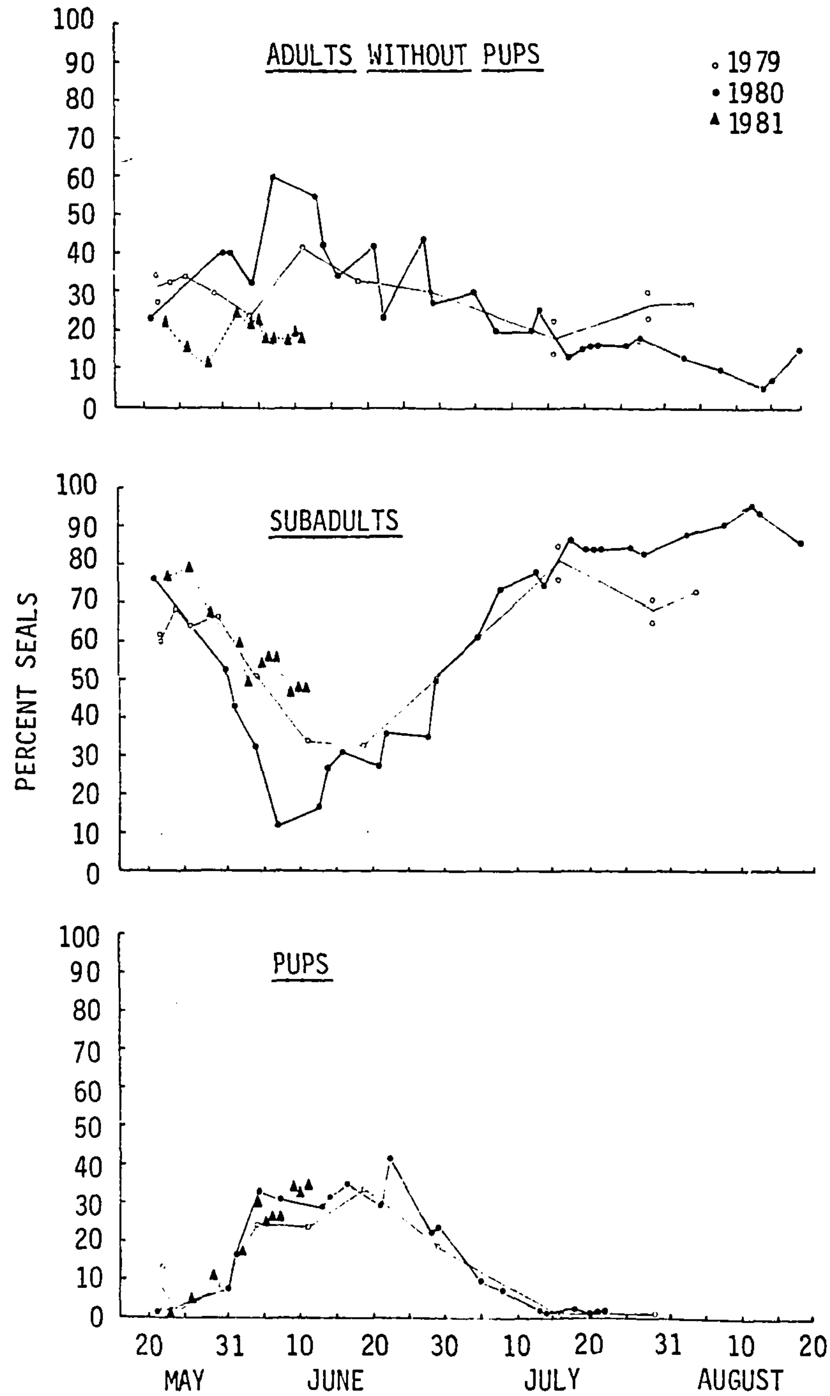

Fig. 13. Seasonal fluctuations in the relative age composition of seals in upper Aialik Bay, 1979-1981.

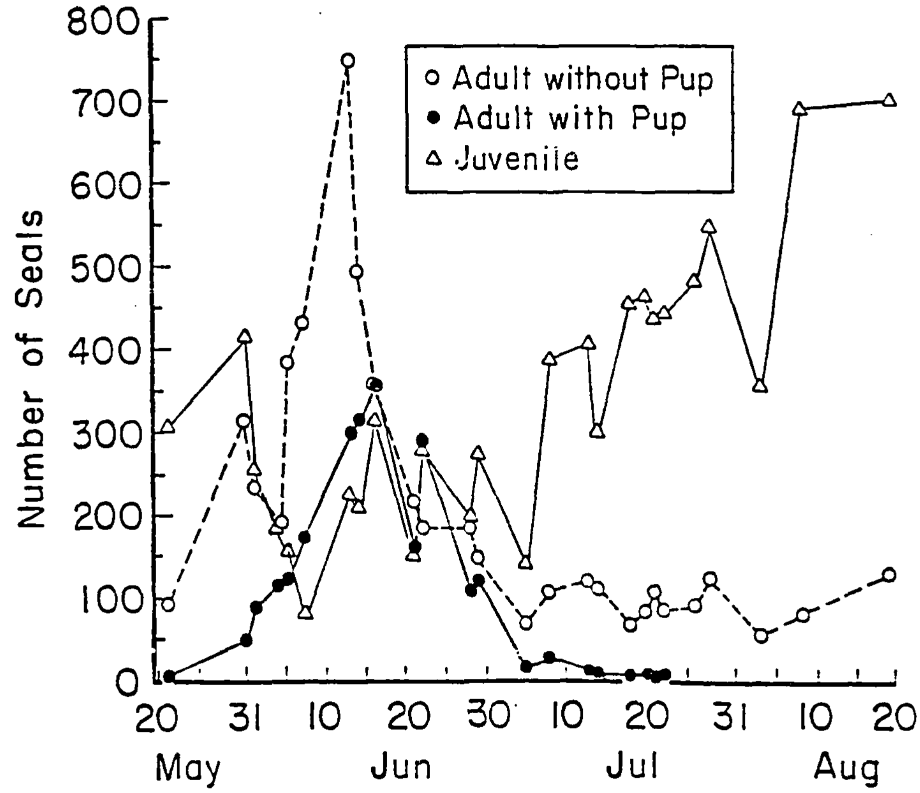

Fig. 14. Seasonal fluctuations in the midday counts of adult harbor seals with pups and without pups and of subadults in Aialik Bay, 1980.

markedly to about 60-90%, while that of the subadults had fallen to its lowest level. In 1980, more than 1,000 adults were seen on the ice, while only about 200 subadults were present. After mid-June, numbers of adults declined steadily, whereas subadults increased in abundance. The adults reached their lowest numbers during the beginning of the breeding period in early July and continued at that low level through August. By early to mid-August, when most of the seals showed signs of hair loss associated with the molt, the subadults increased to their maximum of nearly 700 on the ice, the adults continued in low numbers (fewer than 150).

Natality

The birth of harbor seals in upper Aialik Bay probably begins in the first week of May. This was indicated by the presence of a pup estimated to have been about two weeks old when first sighted on 21 May 1979. Each year, my observations of births showed a bimodal tendency, with peaks about 25 May and 6 June (Fig. 15). The cause of this bimodality is unknown.

To test whether the bimodality might have been related to the age of the mother, females with pups were classified in 1981 as "adults" and "subadults" on the basis of their size. "Adults", were about nine years and older, and generally would have had at least two pups previously; "subadults" were younger seals, most of which were giving birth for the first time. "Adults" made up 50% (SD = 7.8%) of the females with pups sampled during 27 censuses, which is comparable with the 40% predicted by Pitcher and Calkins

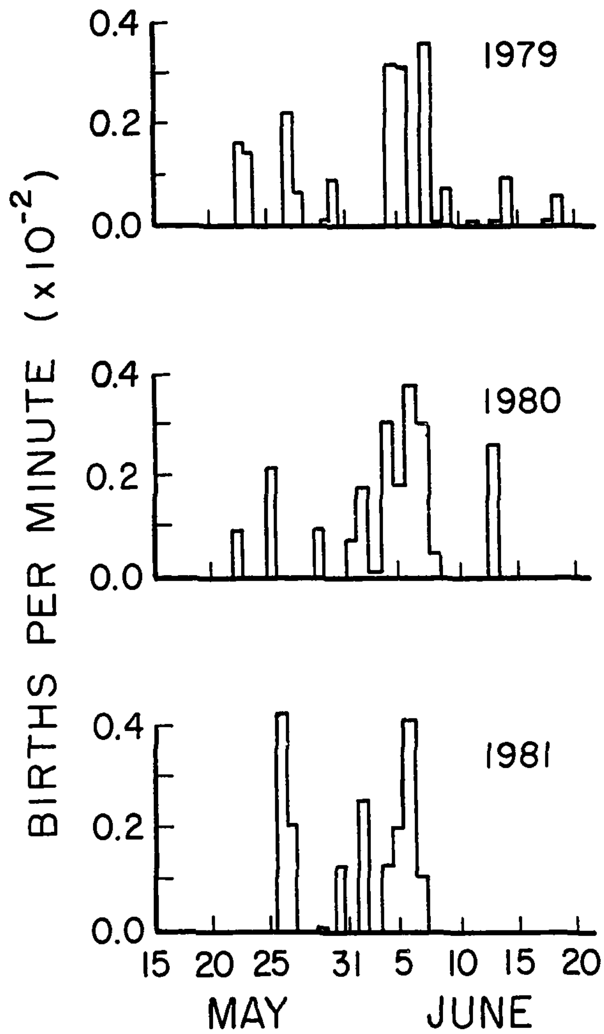

Fig. 15. Frequency of occurrence of births of harbor seals in upper Aialik Bay, 1979-1981.

(1979). The numbers of adults and subadults with pups present between 22 and 28 May were compared with those counted between 2 and 8 June. Differences were not significant (Chi-square Test, $T = 0.007$, $df = 1$, $P > 0.25$), and no tendency for difference was indicated (Table 8).

The pups rapidly increased in abundance after 31 May; greatest numbers were present in mid-June (Fig. 16). In 1979, the number of pups declined between 11 and 14 June, probably due to the effects of strong northwesterly winds in during that period (see below). The last births apparently took place during the second week of July, for a nearly weaned pup about 3 weeks old was sighted on 4 August 1979.

The number of births per hour showed a diel rhythm each year. The hourly rate was higher in the afternoon, evening, and early morning than during late morning and midday (Fig. 17). Because the evidence of a birth occasionally persisted for as much as 2 hours after the birth had taken place, all of the rates in Figs. 15 and 17 may be biased slightly upward. Although they may not reflect the actual birth rates, they were equally biased in the same way, hence are comparable.

Bald eagles (Haliaeetus leucocephalus) and glaucous-winged gulls (Larus glaucescens) quickly reacted to occurrence of a birth. Up to three eagles and 57 gulls were seen on and near a single site of birth, attempting to feed on the placenta, the lanugo pelage, and the amnionic membranes left on the ice. Within an hour after birth,

Table 8. Numbers of adult- and subadult- size females with pups sighted during early (22-28 May) and late (2-8 June) peaks of pupping, Aialik Bay, 1981.

Date	Size of female with pup	
	Adult	Subadult
22-28 May	67	65
2-8 June	1117	1100

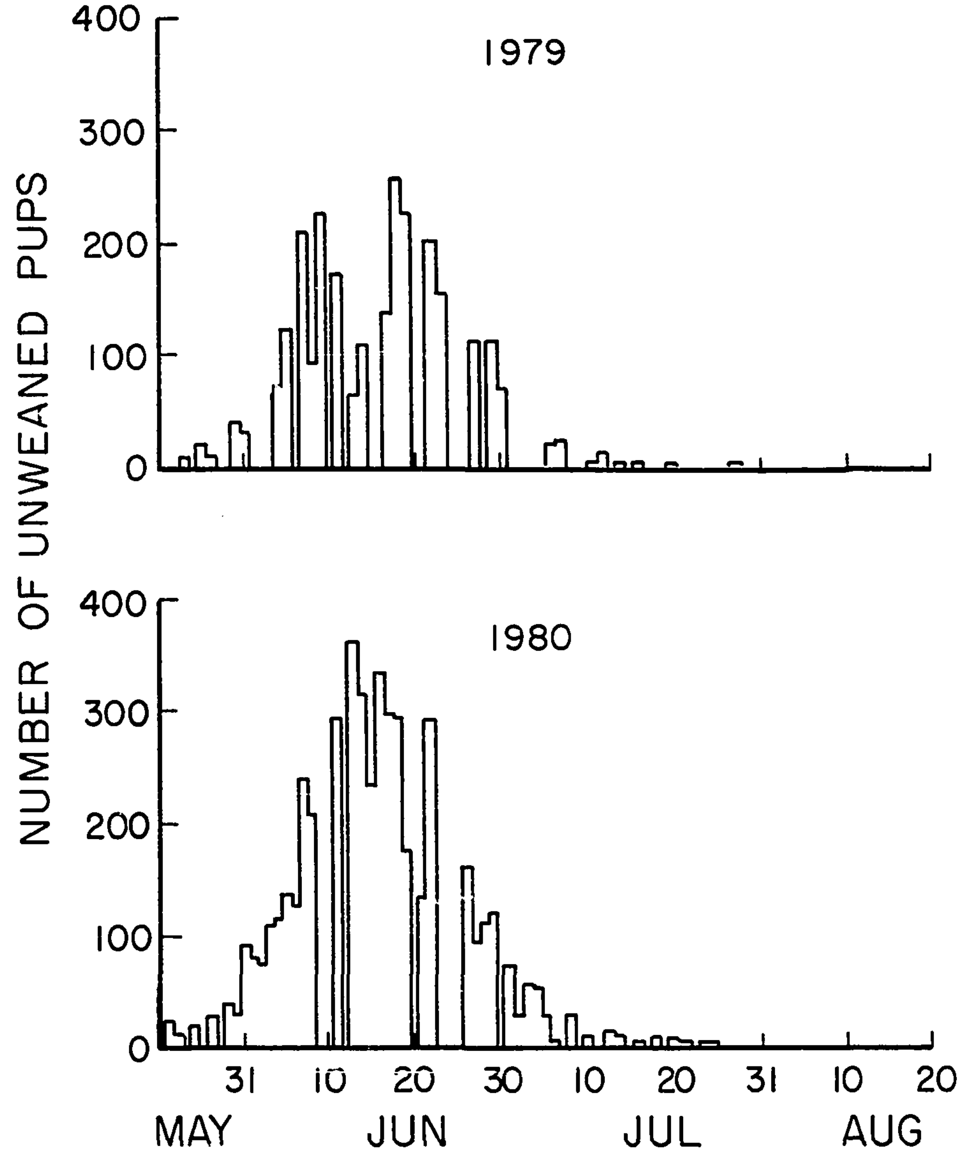

Fig. 16. Seasonal variation in daily abundance of unweaned harbor seal pups in upper Aialik Bay, 1979-1980.

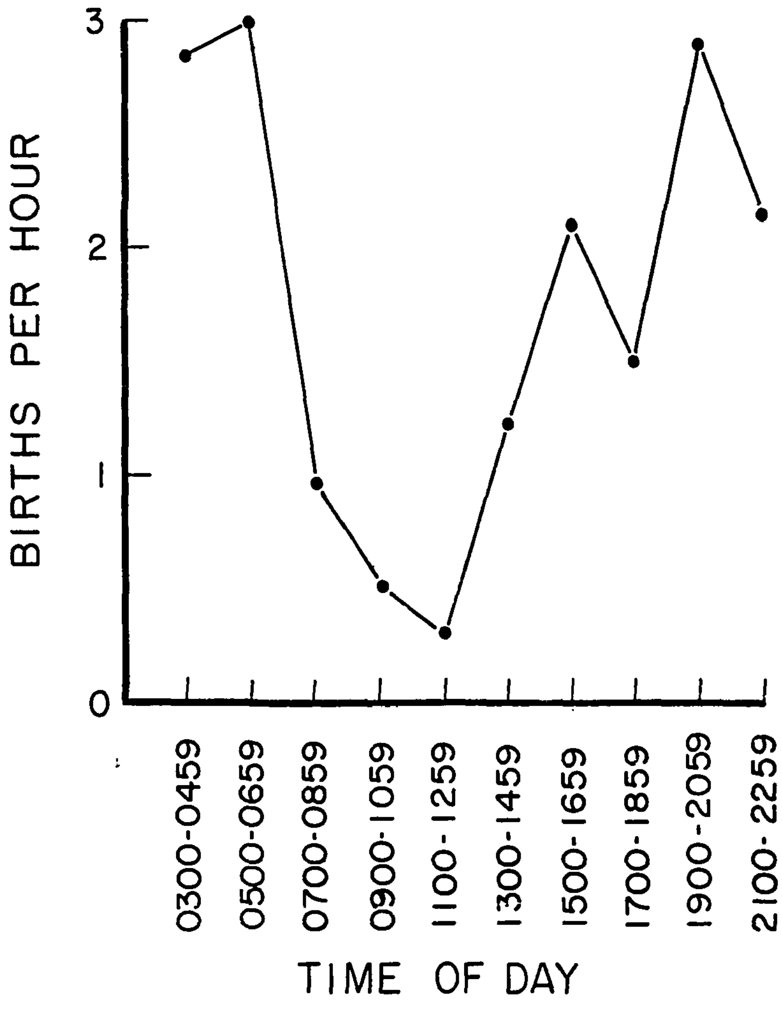

Fig. 17. Diurnal variation in birth rates of harbor seals in upper Aialik Bay, 1979-1981.

the mother generally left the ice and attempted to lead her pup into the water. Often, she had to climb back onto the ice several times to defend the site and her pup from the scavenging birds. Glaucous-winged gulls were the only birds observed to approach the pup closely and occasionally to feed on the attached portion of the umbilicus.

The mother and pup maintained close contact in the water. Occasionally the pup climbed on its mother's back and was carried by the mother; otherwise the mother slowly swam away from the birth site, repeatedly engaging in nose-to-nose contact with the pup. Pups were slow to follow and often required repeated guidance from their mothers. After several minutes in the water, the mother generally led the pup to another berg and hauled out. If the pup was unable to climb up onto the ice, the pup would swim away. The mother then re-entered the water and eventually found a suitable berg, onto which the pup could climb. On the ice, the pup nursed for the first time.

The first definite sightings of weaned pups were on 10 June 1979, 11 June 1980, and 6 June 1981, 20 to 21 days after the beginning of the main pupping season (Fig. 18). The status of a few lone pups that were sighted earlier was not determined with certainty. I believe that they were only temporarily deserted by their mothers, because they had not atained their full weight, but they could have been abandoned. The greatest abundance of weaned pups occurred between 27 and 28 June, 1979 and between 26 and 29

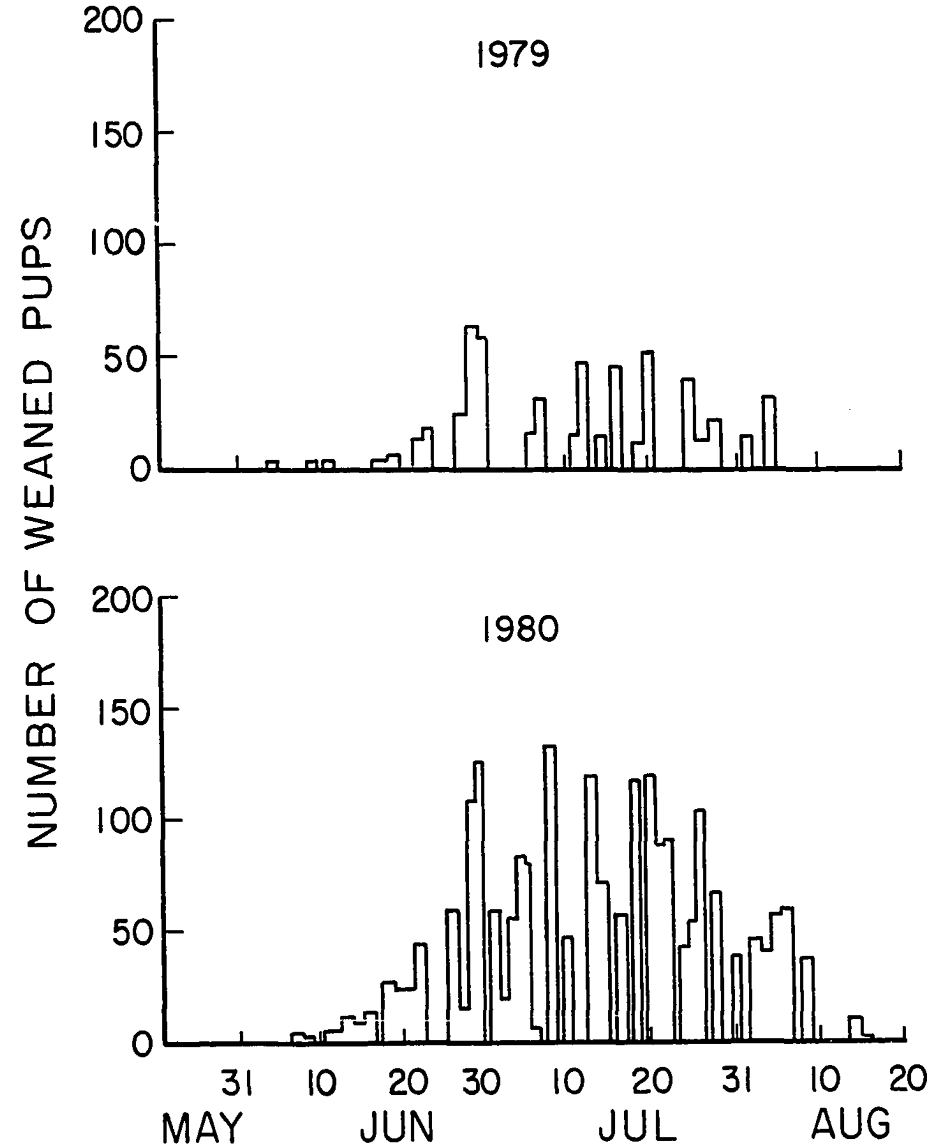

Fig. 18. Seasonal variation in daily abundance of weaned harbor seal pups in upper Aialik Bay, 1979-1980.

June 1980, 23 days after the peak of parturition. Hence, I estimated the average nursing period of harbor seals in Aialik Bay to be 23 days.

Characteristics of Haulout Sites

On shore, birth and post natal care of harbor seal pups often take place in different locations, separate from haulouts occupied by non-breeding herds (Knudtson 1974, Johnson 1974, 1976a, pers. obs.). Females pupping on glacial ice in Aialik Bay also tended to segregate from the non-breeding seals.

Seals gave birth mainly on large bergs more than 5 m in diameter (median, 7 m), while seals with growing pups used slightly smaller bergs, 1 to 5 m in diameter. Conversely, seals without growing pups tended to haul out on bergs 3 to 6 m in diameter (Fig. 19). The differences between reproductive classes in the sizes of bergs used were highly significant (Chi-square Test, $T = 122.08$, $df = 6$, $P < 0.001$). The sites occupied by females at parturition also tended to be separated by greater distances from other seals (Fig. 20) than were those occupied by females with older pups and non-breeding seals (Chi-square Test, density of aggregations: $T = 88.9$, $df = 16$, $P < 0.001$; distance to nearest occupied berg: $T = 38.6$, $df = 6$, $P < 0.001$). Although the density of seal groups tended to increase with the density of ice, females giving birth in low density groups did so in areas of more compact ice than expected (Chi-square Test, $T = 19.8$, $df = 6$, $P < 0.005$). This resulted in a much greater use of 8-okta ice by females at the

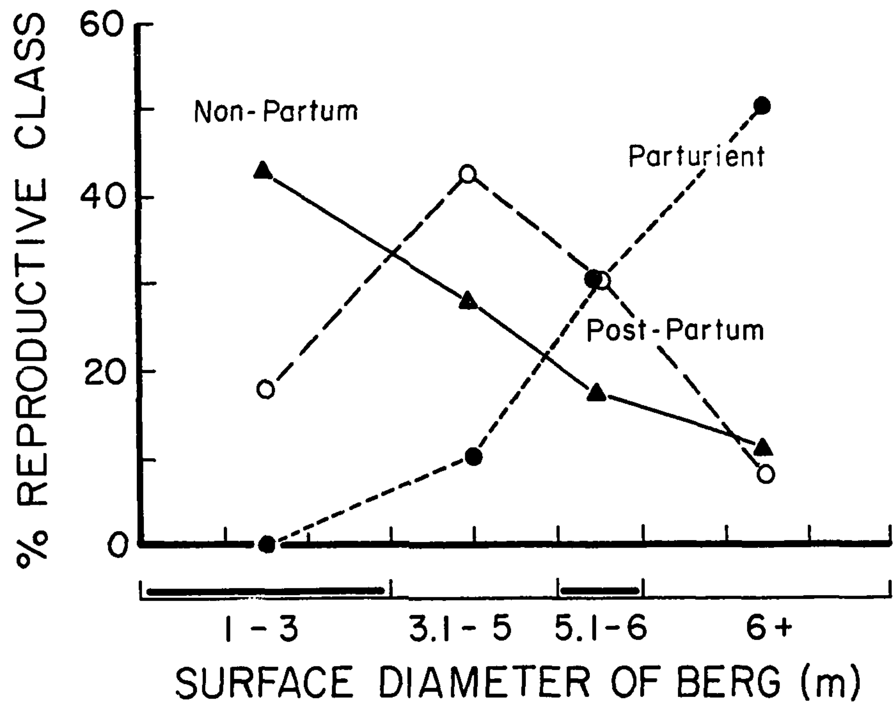

Fig. 19. Surface diameter of bergs used as haulout sites by three reproductive classes of harbor seals in Aialik Bay, 1980.

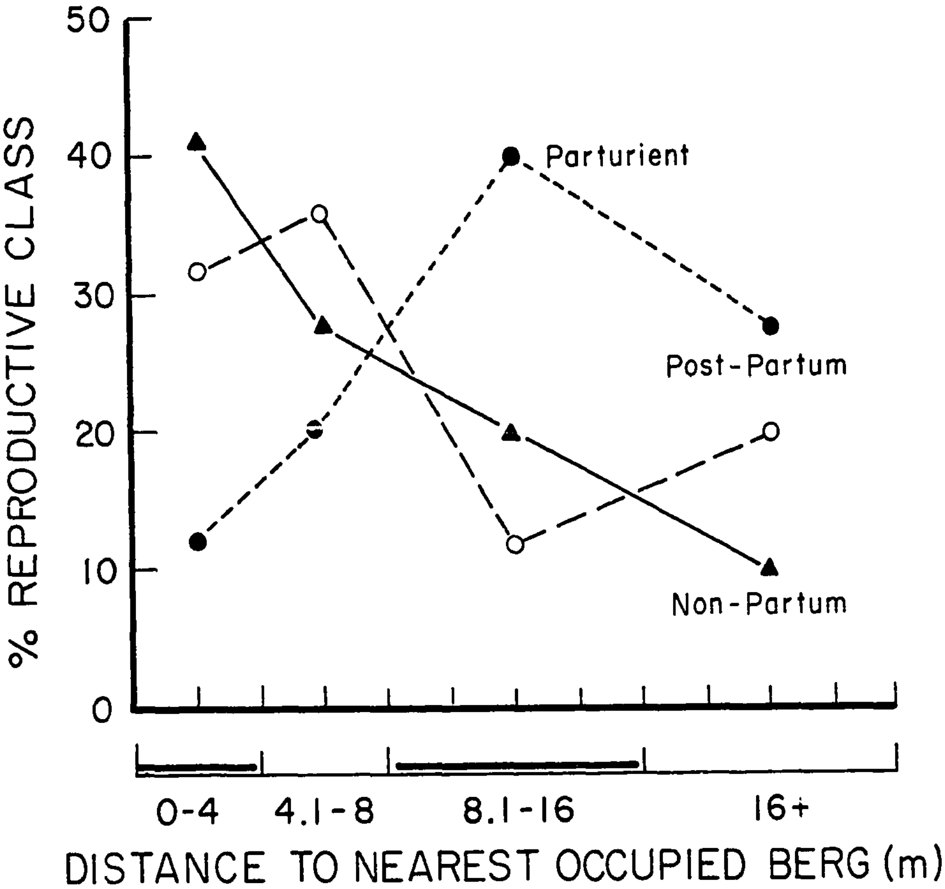

Fig. 20. Comparative distances between bergs occupied by harbor seals of three reproductive classes in Aialik Bay, 1980.

time of parturition than by females with older pups and by non-breeding seals (Fig. 21). By hauling out in low densities in compact ice, they selected for the most stable habitat with minimal potential for disturbance.

Interactions of parturient females with other seals were minimized also by their tending to give birth mainly in evening and early morning, when most of the other seals were in the water (Fig. 17). Females caring for older pups hauled out early in the day, generally in greatest abundance from 0900 to 1300 h (median, 1000 h), rather than in midday.

Females with pups tended to haul out on bergs with other seals much less often than did seals without pups (Chi-square Test, $T = 103.42$, $df = 3$, $P < 0.001$) (Table 9), but females with pups became increasingly tolerant of other seals as the season advanced (Fig. 22). From 21 May to 7 June, the composition of seals present on bergs used by females with pups closely resembled the overall composition of the population (Table 10). From 8 to 24 June, however, when pups were more numerous, females with pups shared bergs less often with other females with pups but tended to be with other adults and subadults in somewhat greater proportion than predicted by the age composition of the population (Chi-square test, $T = 4.82$, $df = 2$, $P < 0.1$). From 25 June to 21 July, females with pups shared their bergs much more frequently than predicted with other adults and much less frequently with subadults (Chi-square test, $T = 10.27$, $df = 2$, $P < 0.01$). In the last period, many of the

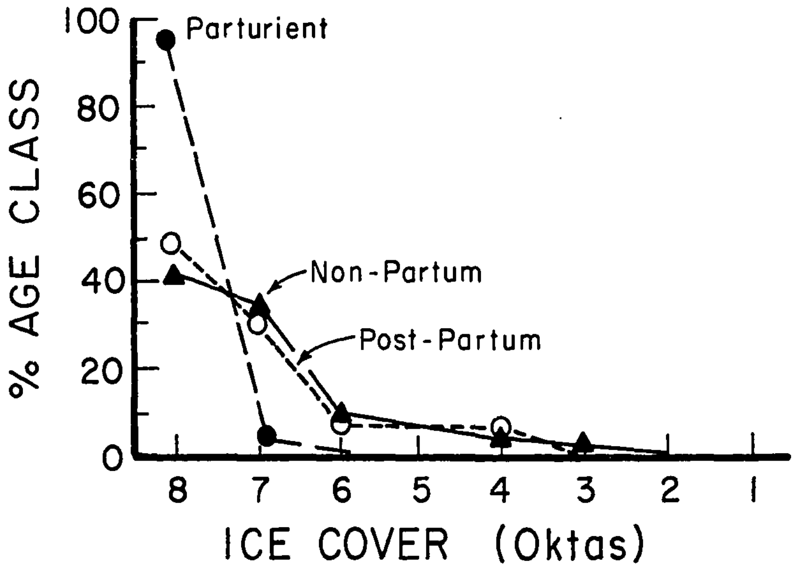

Fig. 21. Comparative densities of ice used by harbor seals of three reproductive classes in Aialik Bay, 1980.

Table 9. Variation in the proportion of each age/sex class observed on bergs with other seals. in Aialik Bay, 1980.

Age	Sharing berg		Not sharing berg		N
	No.	%	No.	%	
Adult with pup	17	8	201	92	218
Adult without pup	107	34	206	66	313
Subadult	349	45	430	55	779
Weaned pup	27	30	62	70	89

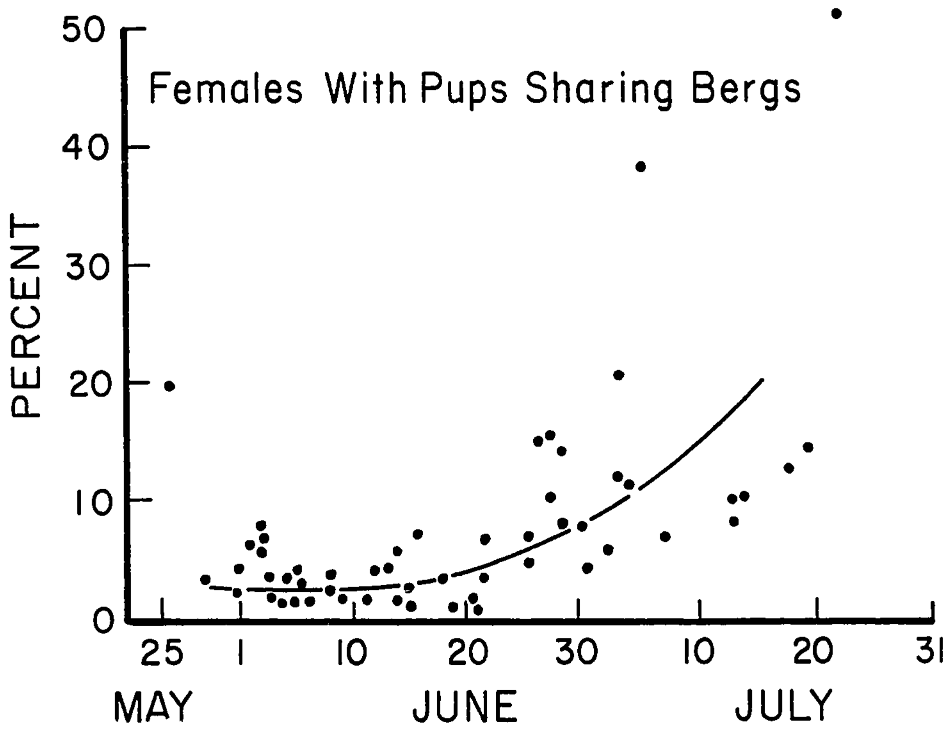

Fig. 22. Seasonal variation in the proportion of females with pups sharing bergs with other seals in Aialik Bay, 1980.

Table 10. Comparison of age-composition of seals sharing bergs with females and pups with that of the population as a whole in Aialik Bay during three time periods in 1980.

Date	Age of seals	Per cent composition of seals		N
		Sharing berg with female and pup	In population	
21 May - 7 June	Adult	39%	37%	24
	Female with pup	29%	25%	18
	Subadult	31%	38%	19
8 - 24 June	Adult	49%	31%	57
	Female with pup	16%	38%	19
	Subadult	34%	29%	40
25 June - 21 July	Adult	62%	25%	46
	Female with pup	11%	8%	8
	Subadult	27%	68%	20

other adults may have been males in search of estrous females, for breeding is believed to have reached a peak during that time.

The density of the aggregations of seals varied throughout the summer (Table 11), as did the ice that they used for haulout areas (Fig. 23). In 1980, three midday censuses randomly selected from four periods (early pupping, post pupping/nursing, breeding, and molting) were analyzed by grouping seals into high, moderate and low density aggregations in high, moderate and low density ice. During early pupping, when ice was abundant (Fig. 24) and few seals were hauled out, seals were dispersed in moderate to low density groups. During the nursing period when numbers of seals were high and ice was moderate in abundance, seals were mostly seen in higher density aggregations. During the breeding season, as ice became depleted and numbers of seals decreased, seals were more dispersed, hauling out in moderately dense aggregations. However, they also hauled out in greater frequency on 4- to 6-okta ice than during the early pupping period. By doing so they were able to maintain greater distances between individuals during the less favorable ice conditions. While molting, seals became more gregarious and hauled out in high densities on 7- to 8-okta ice even though 4- to 6-okta ice was available. Although the density of groups is at least partially a function of the compaction of ice, seals apparently will haul out on less favorable ice in order to maintain greater inter-seal distances.

Table 11. Variation in group density relative to time for seals with and without pups, Aialik Bay, 1980.

Date	Without pups				With pups			
	N	I-II	III-IV	V-VI	N	I-II	III-IV	V-VI
<u>Pupping</u>								
29 May - 1 June	984	26%	46%	28%	120	53%	35%	12%
<u>Nursing</u>								
11-19 June	1416	9%	29%	61%	729	12%	31%	58%
<u>Breeding</u>								
2-8 July	951	9%	84%	6%	64	23%	55%	22%
<u>Molting</u>								
4-16 August	2037	9%	35%	55%				

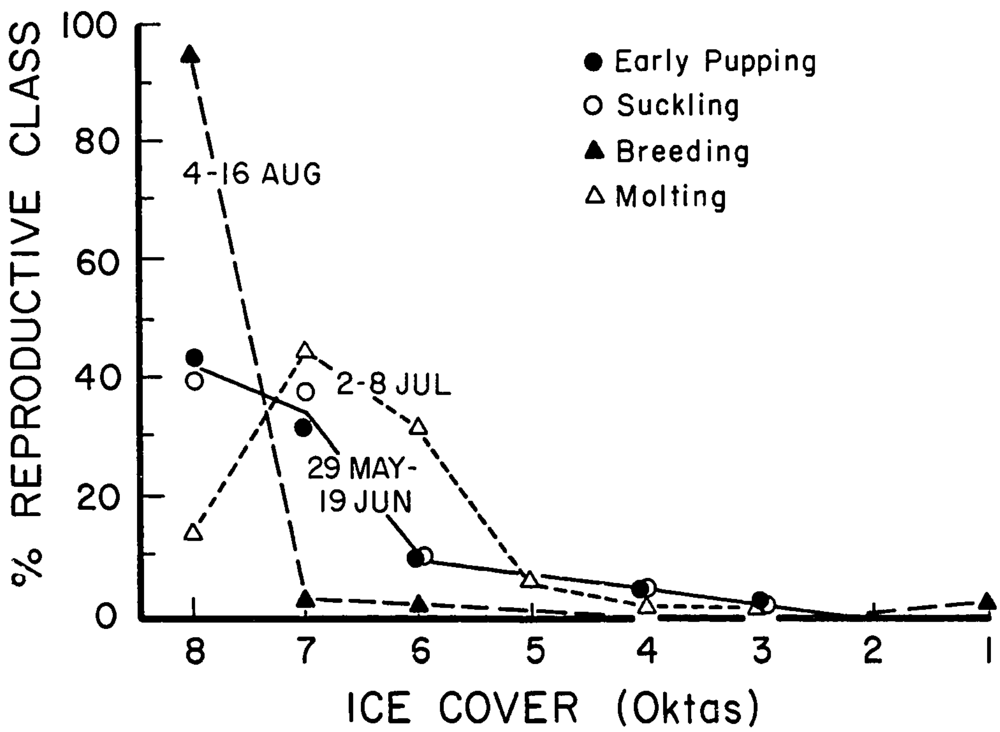

Fig. 23. Seasonal variation in the ice cover surrounding haulout sites during early pupping, post-partum suckling, breeding and molting in Aialik Bay, 1980.

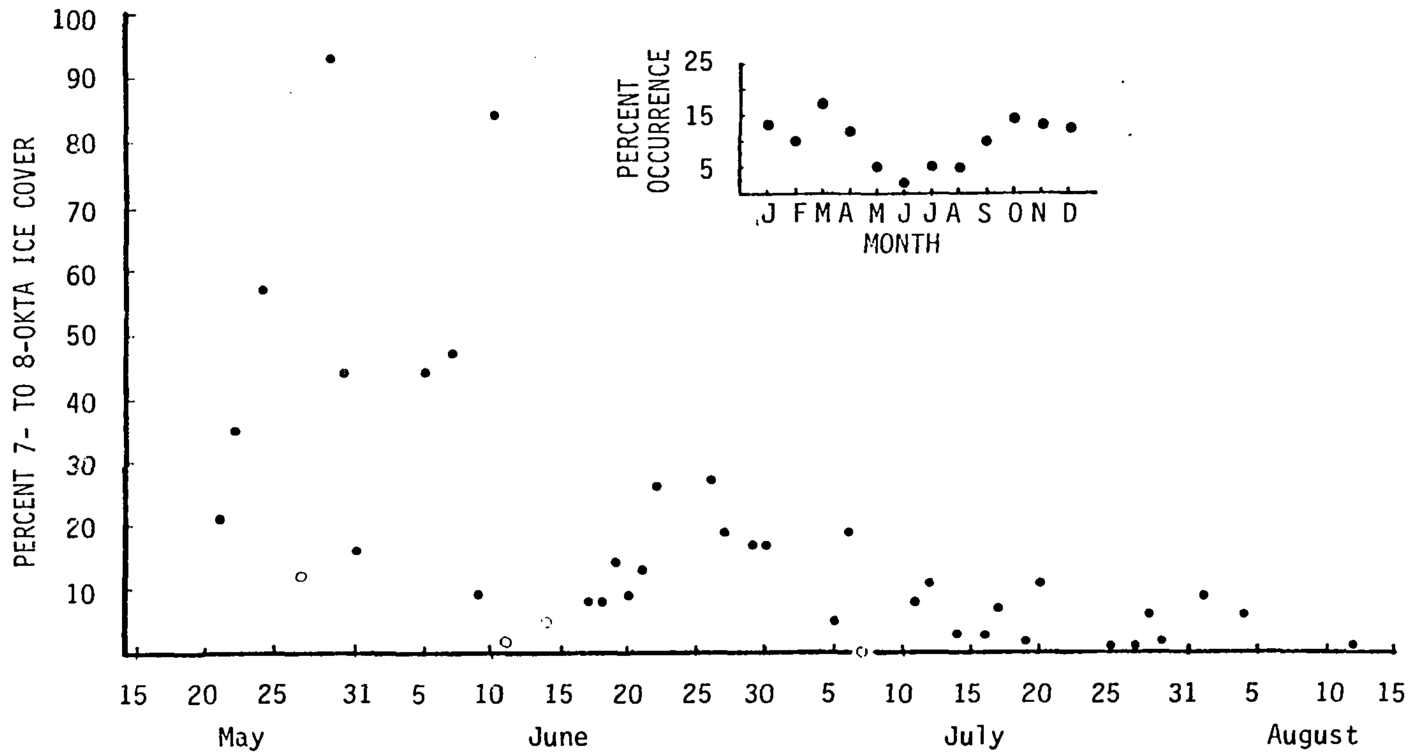

Fig. 24. Seasonal variation in percent of area north of Slate Island covered by 7- to 8-okta ice during 1979. Open circles represent ice cover during times of strong northwesterly winds. The small graph shows seasonal variation in frequency of occurrence of strong northwesterly winds along the Kenai Peninsula (Brower et al. 1977).

Pup Mortality

Mortality of pups in Aialik Bay was difficult to document. Although there was wide variation between years in the numbers of pups weaned, there was no evidence of extensive pup mortality during the weaning period in any year. In both 1979 and 1980, from 27 May to 29 June, several lone pups were sighted, but their status was difficult to determine until they began to show signs of starvation. In 1979, three of at least six lone pups were marked on Squab Island. These marked pups remained alone and stayed near the island for at least one to three days before they disappeared. Lone pups often were on bergs occupied by one or more females with pups. The lone pups were allowed to remain on the berg but were treated with hostility whenever they approached any of the other animals. Abandonment of pups appeared to be much lower in 1980 than in 1979. During both years the maximum number of lone pups was counted on or about 19 June, late in the suckling period; another lower peak occurred in late May and early June (Fig. 25). At Tugidak Island, Bishop (1967) observed that abandonment of pups appeared to reach its maximum in May, before the June peak of pupping, and that most of the abandoned pups were newborn. The increase in lone pups I sighted in Aialik Bay may have been due to temporary abandonment by the mothers, which commonly takes place just prior to weaning (Johnson 1976a, Hoover, pers. obs.). In Aialik Bay, I did observe some instances of lone pups that definitely were due to temporary separations. As the pups grew older, they occasionally entered the

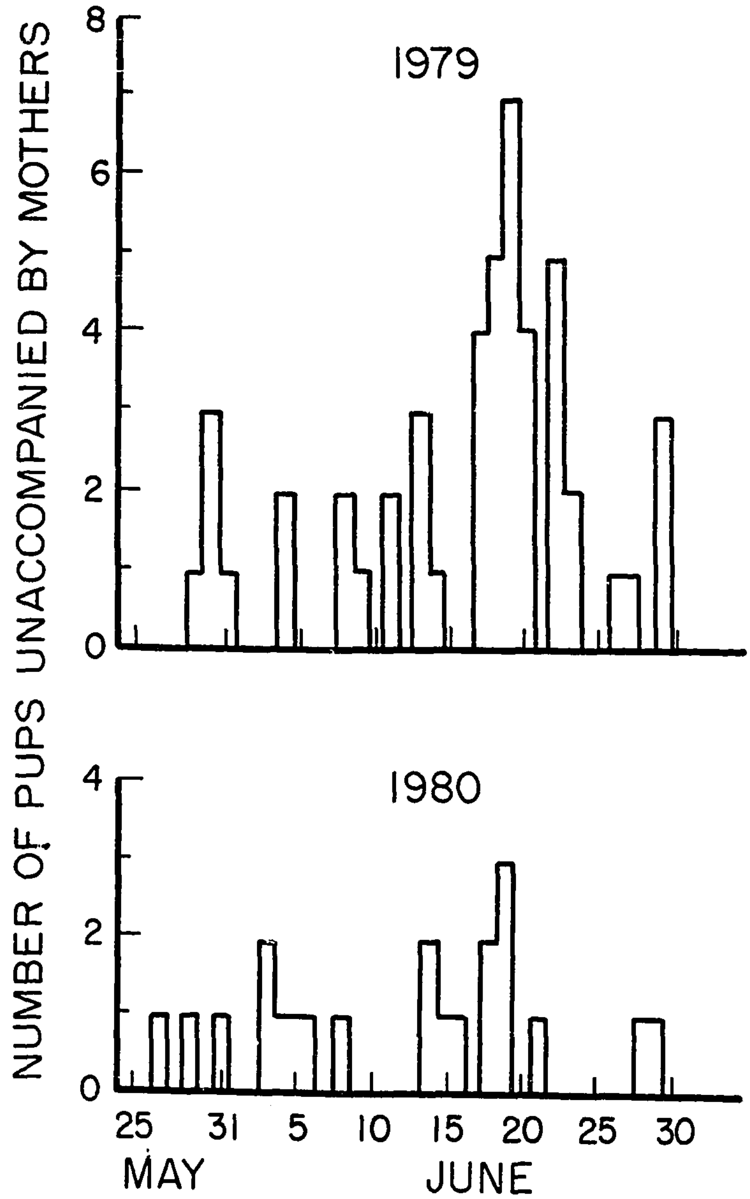

Fig. 25. Seasonal fluctuations in the number of pups less than three weeks old that were unaccompanied by their mother in Aialik Bay, 1979-1980.

water and swam, while their mother rested on the ice. Furthermore, mothers occasionally left their pups on the ice for several hours before returning to reclaim them.

From 11 to 14 June 1979, ice for hauling out was unavailable to the seals, because strong northwesterly winds had blown most of it out of the upper bay. During that time, six lone pups and three mother-pup pairs were seen to use rocks and islands as haulout sites; the rest of the animals apparently remained in the water. Pups in the water were very vocal at that time, and the number of lone pups sighted increased markedly thereafter. The number of lone pups seen during 1979 was about double the number seen in 1980 (Fig. 25), suggesting that early separations of mother and pup took place much more frequently in 1979. Coincidentally, the peak number of successfully weaned pups in 1979 was about half of that recorded in 1980 (Fig. 18). Since the number of pups born in 1979, up to the onset of the period of high winds, was similar to that in 1980 (Fig. 16), I suspect that the stress resulting from lack of ice had a strong negative influence on survival of pups less than a week old. Probably, the incidence premature separations of mother and pup increased and resulted in an increased occurrence of starvation of pups. The probability that mother-pup pairs moved to other locations seems low, because ice also was dispersed from all of the other tidewater glaciers in the region. At the same time, local fishermen reported no major concentrations of seals along the shoreline or on offshore islands, elsewhere in the region.

Breeding Behavior

Adult female harbor seals enter estrus about one week after weaning their pup (Bishop 1967, Bigg 1969a). Pitcher and Calkins (1979) estimated that the mating period for harbor seals in the Gulf of Alaska extends from mid-June to late-July. In Aialik Bay, an influx of large adult seals took place each year in early June, and about that time I observed occurrences of behaviors generally associated with breeding, such as slapping the water with fore- and/or hind-flippers and repeated dives in conjunction with underwater exhalation (cf. Venables and Venables 1957). If ovulation takes place one week after the pup has been weaned, estrus in Aialik Bay would begin during the third week of June, reach a peak in the first week of July, and be completed by the first week of August. In both 1979 and 1980, the number of seals using the ice declined markedly in late June, reached a low during the first week of July, and remained low to mid-August.

I was not able to determine the location in which most of the breeding took place, but I observed two intraspecific interactions suggestive of breeding behavior in 1980. first took place in Pederson Lagoon; the second was observed just north of Squab Island. Although copulation was not seen in either of those interactions, I describe them here to provide information for potential future evaluation.

At Pederson Lagoon, seals were heard flipper-slapping almost every night between 10 and 16 June. At 2300 h on 17 June, two adult seals of unknown sex were interacting intensively in shallow water about 5 m from shore. When first observed, they were engaged in "rolling pair" behavior (Venables and Venables 1957, Sullivan 1981), oriented vertically, face-to-face, then submerging and resurfacing. In this process, one or both of them "snorted" (a highly exaggerated exhalation of air, often, if not always, done with the nose partially submerged), occasionally spraying water into the air. After snorting several times, one of the seals slowly swam away at the water's surface for a few meters, then dove and swam back; meanwhile, the other remained passive, floating in one location. This sequence was repeated at least twice. Both seals subsequently swam farther offshore, then approached each other within a few centimeters, nose-to-nose. As one sank underwater, the other followed. About one minute later, they resurfaced — one snorting and the other calmly swimming around it. The snorting seal dove, apparently swimming out of the lagoon, while the other slowly swam along the perimeter of the lagoon, its head above the water's surface. The entire sequence lasted at least 15 minutes, in which time two other seals were heard in the lagoon: a vocalizing pup and an older seal, flipper-slapping at the northern end of the lagoon.

At 1241 h on 22 June, the second possible breeding encounter was seen near Squab Island. A very large adult male entered the water from a berg that, was occupied by a female with a 2- to 3-week-old pup and a small subadult. The male surfaced 2 m downwind of another berg occupied by a sleeping female with a nearly weaned pup. The male remained alongside the berg, with head above water, eyes half-closed, and nostrils open. The female awoke and began flipper-waving and vocalizing loudly. The male continued floating quietly near the berg. The pup began to crawl around, and the female responded aggressively, biting at the pup. The female then slid into the water, and subsequently surfaced facing the berg. As the male sank below the water's surface, the female followed him immediately and they were lost from view. The pup entered the water soon after the female and swam around the north end of Squab Island, apparently in search of its mother. I did not see the female and her pup reunite.

In the second instance, the male appeared to orient to the female olfactorily. He did not enter the water until she was upwind of him, and his nares were almost always open while he was downwind of her. He did not attempt to crawl out on the female's berg or to "rush and grab" her in the water, as Bishop (1967) described. The female responded aggressively at first by flipper-waving and vocalizing until she entered the water. No snorting was heard from either seal.

On 2 July, the male from the second interaction was resighted during a 105-min observation period. Throughout that period, he was seen repeatedly in a patch of 3-okta ice about 60 m in diameter, adjacent to an aggregation of 172 seals on 8-okta ice. On three occasions he was observed to displace seals from the area. The first time. he surfaced and snorted, vocalized, and lunged at a subadult. They both submerged, rolling and chasing; at least one of them was blowing bubbles under the water. The adult, becoming aware of my presence as it surfaced, slapped the water with a foreflipper and dove again; the subadult also dove. Soon thereafter, the adult resurfaced and swam slowly about the 3-okta opening. The subadult was not seen again. About 30 min later, the adult surfaced again at the same time as another seal. They rolled and scratched at each other with their foreflippers and bit at each other's neck. This fight, lasting less than 30 s, was terminated when the second seal dove, apparently leaving the area. The adult slowly dove, slapped the water with his hind flippers, and continued to patrol the area. About 25 min later, two subadults swam into the open area. The male rapidly pursued them across it until they reached the 8-okta ice; no further chase was given. These encounters and their confinment to the patch of 3-okta ice, adjacent to the large herd, suggested that the male was defending a territory, excluding certain other seals from the area. Unfortunately, I was unable to determine the sex of the displaced seals, but three of the four were small, subadult-sized animals, probably not old enough to have been estrous females or breeding males. Although the location of this "territory" moved with the drifting ice, it remained stable relative to the position of the main group of seals resting on the ice.

Molting

The shedding of hair by seals in Aialik Bay was noticed from 16 July to the end of observations in August. Before that period, in both 1979 and 1980, I observed that the number of subadult seals using the ice as a haulout increased markedly and continued to increase into mid-August. An influx of very small seals, probably 1 year old, began on 19 June in 1979, and the number of older subadults increased after 6 July in 1980. In 1980, 50% of the seals had shown signs of hair loss by 3 August (Fig. 26); the first completely molted seals were seen on 26 July. By 3 August, about 10% of the subadult seals sighted on the ice were completely molted. Since that proportion did not increase thereafter, I presume that the subadults were leaving the area after their molt was completed. These findings suggest that the subadults began to haul out with increasing frequency about 2 weeks prior to hair loss, and that their use of the ice declined after they were completely molted.

As noted earlier, the number of adults counted in upper Aialik Bay declined after the pupping period. Possibly, they returned to the upper bay in late August-September to molt, or they may have gone elsewhere. Since the numbers of adults showing less than 50% hair loss declined after 8 August, in a manner similar to subadults (Fig. 26), I believe that the adult seals that molted in Aialik Bay did so on a schedule similar to the subadults. A later influx of adults seems unlikely; I suspect that most of the adults that came to Aialik Bay for the pupping season went elsewhere to complete their molt, probably because of the decreasing availability of ice in late summer.

In 1979, when ice was scarce in August, seals often were seen

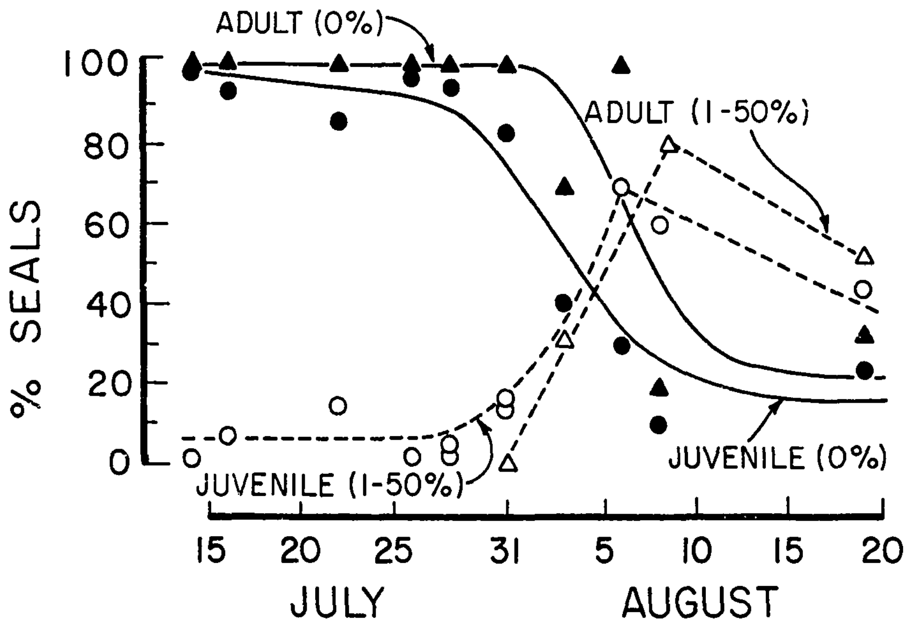

Fig. 26. Seasonal variation in the proportion of unmolted (0% molt) seals and seals in early stages of hairloss (1-50% molt) sighted on the ice in upper Aialik Bay, 1980.

swimming near the glacier, apparently waiting for ice to be calved. At that time in 1980, ice was abundant, and seals swimming at the foot of the glacier were few. Even with the better ice conditions in 1980, however, adults still were scarce during the molt, relative to subadults. By molting in other localities, adults could reduce the competition for space on the ice, which at that time of the year seems unpredictable in amount.

Potential Prey

The major concentrations of harbor seals in upper Aialik Bay occurred during pupping and molting, which are periods when feeding tends to be reduced (Pitcher and Calkins 1979, Ashwell-Erickson and Elsner 1981). A fisherman who previously had hunted seals in the area said that the seals killed near the ice almost always had an empty stomach, whereas those on the outer coast, near the Chiswell Islands, usually had fed recently. I saw no evidence of feeding near the ice.

I often saw seals apparently feeding during rising tides in Pederson Lagoon. This feeding behavior was seen primarily along the interface between the incoming waters from Aialik Bay and the estuarine waters of Pederson Lagoon. Arctic terns (*Sterna paradisaea*) and mew gulls (*Larus canus*) also fed along that interface. I do not know the kind of prey the seals were taking, but the finding of a herring (*Clupea harengus*) adjacent to a nearby tern's nest indicated the presence, at least, of that species. I also saw a female harbor seal with a pup apparently feeding in

Phocoena Bight on 3 June, near two harbor porpoises (*Phocoena phocoena*), which also appeared to be feeding. The only definite evidence of feeding was seen on 20 August 1981, when a seal surfaced with a flatfish (Pleuronectidae) off the southern end of Pederson Spit.

Samples of the local marine fauna were collected during winter and summer by T. C. Carpenter and me, in connection with a study of marine productivity in glacial fjords (Carpenter, in prep.). Potential prey of harbor seals were identified in those samples (Table 12). Pollock were caught in each of the otter trawls and appeared to be one of the dominant demersal fishes, as were longsnout pricklebacks. During the summers, red and pink salmon and dolly varden trout were numerous. Other fishes were present in smaller numbers. Most abundant of the invertebrates were the shrimps *Pandalus borealis*, *P. goniurus*, *Pandalopsis dispar*, and *Crangon communis*. Although the sampling methods did not allow accurate quantitative assessment of each species, they did indicate that several types of prey known to be commonly eaten by harbor seals elsewhere were numerous in Aialik Bay when the seals were abundant there.

Table 12. Potential prey of harbor seals observed and collected in upper Aialik Bay, 1979-1982.

Fishes	Season[a]
Gadidae	
Walleye pollock (_Theragra chalcogramma_)[b]	S/W
Clupeidae	
Pacific herring (_Clupea harengus_)[b]	S/W
Osmeridae	
Eulachon (_Thaleichthys pacificus_)[b]	W
Capelin (_Mallotus villosus_)[b]	S/W
Pleuronectidae	
Yellowfin sole (_Limanda aspera_)	S
Flathead sole (_Hippoglossoides elassodon_)[b]	S/W
Pleuronectid unidentified	S
Cottidae	
Sculpin - several unidentified species[b]	S/W
Salmonidae[b]	
Red salmon (_Oncorhynchus nerka_)	S
Pink salmon (_Oncorhynchus gorbuscha_)	S
Dolly varden (_Salvelinus malma_)	S
Stichaedae	
Longsnout prickleback (_Lumpenella longirostris_)	S/W
Daubed shanny (_Lumpenus maculatus_)	S
Zoarcidae	
Lycodes sp.[b]	W
Cyclopteridae	
Snailfish - unidentified	S
Teleostei larvae	W

Table 12. continued.

Invertebrates	Season[a]
Arthropoda	
Crustacea	
Shrimps[b]	
Pandalus borealis	S/W
Pandalus hypsinotus	S/W
Pandalus goniurus	S/W
Pandalus platyceros	S/W
Pandalopsis dispar	S/W
Lebbeus groenlandicus	W
Lebbeus sp.	W
Eualis biunguis	W
Eualis avinus	W
Eualis suckleye	W
Spirontocaris arcuata	W
Crangon communis	S/W
Pasipheae pacifica	W
Euphausiids	
Euphausia pacifica	S/W
Thysanoessa spp.	S/W
Mysiids	
Neomysis rayii	S/W
Mollusca	
Octopus	S

a. S = mid-May through mid-August; W = December.
b. Prey of harbor seals in the Gulf of Alaska (Pitcher and Calkins 1979).

DISCUSSION

Population Assessment

The actual number of seals residing in any natural setting is difficult to estimate. The number of seals that can be counted on the haulout appears to depend on the amount of space available, the weather, tides, time of day, season of the year, and the age, sex, health, reproductive condition, molt, and other peculiarities of the individuals. These factors, together with the kinds and quantities of foods available, interact to determine the seal's activity pattern and often have very local and disparate influences.

In order to census seal populations in a cost-effective manner, systematic surveys usually are conducted via aircraft or boat. An effort usually is made to conduct those surveys at times when the greatest numbers of seals are expected to be on the haulout (e.g., during low tides, in fair weather, while seals are pupping or molting, see Everitt 1980). The need to survey large areas, however, often does not allow optimal survey conditions for all haulouts. Furthermore, activity rhythms of seals may vary widely within a large survey area, and optimal conditions for census of one site may be very unfavorable for census of another nearby (e.g., see Calambokidis et al. 1978).

Inherent in systematic surveys are the assumptions that there is (1) similarity in the movement of seals in and out of survey areas between surveys, (2) similarity in environmental factors affecting the number of seals hauled out or that differing factors can be accounted for, (3) uniformity in survey techniques between years. Because systematic surveys often encompass areas where environmental effects on haul-out patterns of seals are unknown, some of those assumptions may be violated. This may be especially important if factors affecting the number of seals on the haulout are interactive, that is, if more than one factor influences the seals' haul-out rhythm.

In Aialik Bay, I found strong seasonal variation in the number and age composition of seals hauled out on the ice. Seals counted during the pupping period were not the same seals as those counted during the molt, even though the numbers counted were similar. The number of seals hauled out also varied with environmental conditions. As availability of haulouts was not dependent on tides, the number of seals on the ice showed little variation with tides. Conversely, the number of seals on the ice varied markedly with time of day and was influenced also by weather, especially high winds and the number of days preceding and following storms.

Previous to this study, estimates of the number of seals in Aialik Bay, based on brief aerial and boat surveys, range from 400 to about 600 (Bishop 1967, Bailey 1976, Pitcher and Calkins 1979, F. H. Fay, pers. comm.). The greatest number of seals I counted during 1979-1981 was 1,633 which represents an unknown proportion of the seals inhabiting the upper bay. That count was taken in mid-June, when adults were abundant and subadults were minimally represented;

subadults were preponderant in August. A better estimate of the population can be derived from the sum of the maximum number of pups and adult-sized seals (counted on 13 June 1980) and the maximum of subadults (counted on 8 August of the same year). This yields an estimated total population of 1,944 seals, more than three times the highest estimate from the aerial and boat surveys. Another approach for estimating the population is calculation from the number of pups born. The highest count of pups in Aialik Bay was 358 in 1980. To obtain an estimate of the actual number born, I multiplied that count by 3.8, which is a factor derived from Bishop's (1967) maximal count of 1,059 pups at Tugidak Island divided into the known 4,000 pups killed there by hunters in the same year. The result was 1,360 births and the size of the seal population needed to produce that number, based on the life-table in Pitcher and Calkins (1979) would be 6,265 seals. This is more than three times the best estimate from the repeated counts and an order of magnitude greater than the highest estimate from the aerial and boat surveys. Obviously, sporadic surveys tend to underestimate the number of seals using a particular area. Even repeated counts over long periods do not provide a full assessment, because of the steady turnover of seals, as indicated by changes in age composition.

Over the three years of the present study, I found that counts taken during the second week of June, when the highest numbers of seals were present, were of markedly different age and reproductive classes. In that period in 1980, adults without pups made up 60% of the seals, whereas in 1981 they made up less than 20%; conversely, subadults comprised 12% of the seals in 1980 and 58% in 1981. Adults with pups made up a similar proportion of the seals in those counts each year. Since females with young pups haul out during less satisfactory weather and tidal conditions than the other seals (Johnson 1976a,b), counts taken during early June are likely to represent a consistently greater proportion of adults with pups than of other classes.

Harbor seals are opportunists and show great adaptability in behavior with variations in their environment. If seal populations are to be censused effectively, the pecularities of each population must be determined; population estimates must not be based on generalities about the species. Surveys covering large geographic areas certainly will underestimate the number of seals present, even to the point that they may be misleadingly conservative, unless more attention is paid to the peculiarities of local segments of the population. Even with knowledge of the factors affecting haul-out activities of seals, it is difficult to apply that information to the findings of systematic surveys. Most multivariate techniques require normally distributed, continuous data and cannot accomodate circular functions and categorical data such as time of day, tidal cycles, and weather. The multi-way frequency table analysis (Dixon 1981) is a multivariate technique which shows promise for quantification of such data.

Comparative Ecology of Aialik Bay Harbor Seals

The nearshore littoral and sublittoral zones are among the most diverse and rapidly changing of marine environments (Cushing and Walsh 1976, Ray 1981a). Nearshore areas are subject to wide fluctuations in salinity, temperature, nutrients, and turbidity, as a result of storms, tides, currents, and freshwater input from shore. Organisms in this environment must be tolerant of change or capable of rapid colonization of areas re-structured by catastrophic events. Marine mammals are among the least adaptive of the organisms inhabiting the nearshore zone. Their reproductive output is low, typically 10 offspring or less in a lifetime, and parental investment is high. The life histories of all marine mammals generally fit that of K-selected organisms as outlined by Pianka (1970) and Wilson (1975). Nevertheless, as Ray (1981a) observed, an r- to K-selection gradient also is evident within the spectrum of marine mammals, in that reproductive output may differ by an order of magnitude between species. Ray (1981a) compared marine communities and life-history strategies of several species of marine mammals and found that nearshore species tend to have broader diets and higher reproductive rates than do those in more stable, offshore communities. Of the species compared, the harbor seal is the most r-selected, hence the most versatile. Harbor seals have a comparatively small body size, rapid development, early reproduction, and a high reproductive output relative to many other marine mammals. Because of their diverse diet, intraspecific and interspecific competition are minimized. These traits allow populations to recover rapidly from depletion from natural or man-made causes and gives individuals the ability to colonize diverse habitats, even intruding into man-made environments (Calambokidis et al. 1978).

Timing of Parturition

The time of birth of harbor seals varies geographically around the North Pacific, being earliest in Mexico and latest in the eastern Bering Sea (Fig. 27). The seals in Puget Sound are aberrant in that they have an unusually broad range of birth dates, from June to November (Calambokidis et al. 1978). The timing of implantation, therefore of birth, appears to be genetically controlled by the photoperiod (Bigg and Fisher 1975). and Bigg (1973) and Shaughnessy and Fay (1977) have suggested that variation in pupping times may be adaptively related to the timing of greatest availability of prey used by the newly weaned pups.

One might expect differences in pupping times between dissimilar marine habitats, where the kinds and quantities of prey are likely to differ (Bigg 1969b). A comparison of pupping times at three very different types of haulout sites in Alaska, however, does not support that view (Table 13). The haulout on Tugidak Island, just south of Kodiak Island, has a steeply sloping, rocky beach exposed to the deep water oceanic system of the Gulf of Alaska; the haulouts in the Copper River Delta are on mudflats and barrier islands adjoining shallow estuarine and coastal waters; the Aialik

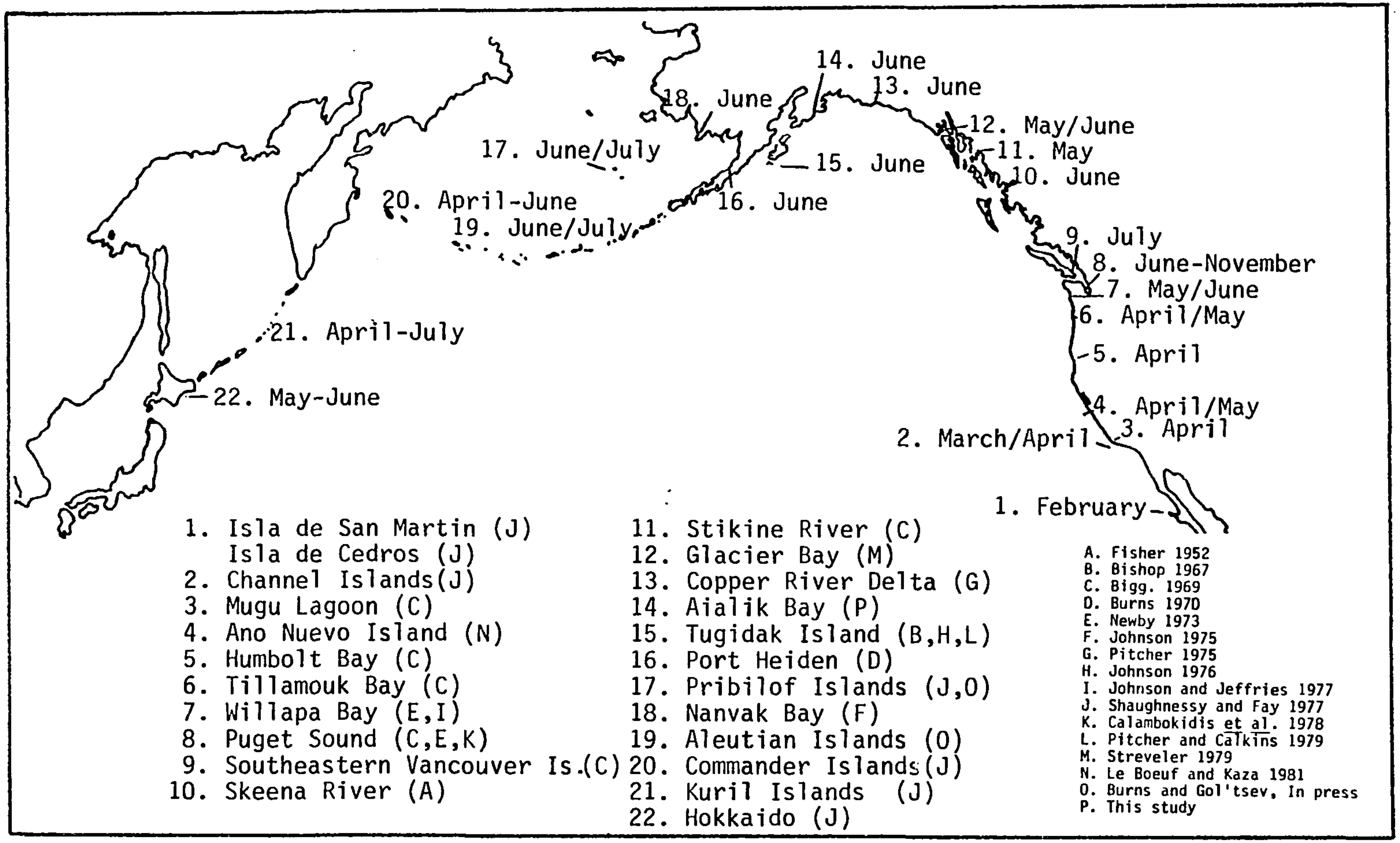

Fig. 27. Clinal variation in the timing of parturition in harbor seals in the North Pacific Region.

Table 13. Comparison of the timing of parturition for three pupping areas in the Gulf of Alaska.

Location	Date of highest rate of parturition	Reference
Copper River	1st week of June	Pitcher 1977
Aialik Bay	4-7 June	This study
Tugidak Island	14-15 June	Johnson 1976b Pitcher and Calkins 1979

Bay haulout is on glacial ice, located in a deep, sheltered fjord. Because of the great disparity between them in the types of environments and haulout substrates, one might expect wide variation among them in time of birth. In all three areas, however, pupping takes place in May to late June or early July, consistent with the timing in other parts of the Gulf of Alaska. The only deviation is that, at Tugidak Island birth tends to be about one week later than in the other areas.

The diet of the adult seals differs regionally, hence that of the weaned pups also may vary between localities (e.g., see Table 2). Pupping in the Copper River Delta coincides well with the May-June run of eulachon (Imler and Sarber 1947) and, as noted earlier, shrimp and pollock appear to be the most abundant prey available in Aialik Bay in June. In Alitak Bay, 25 km northeast of Tugidak Island, capelin and herring are present in maximal numbers in March but are minimally represented in July; pollock are most abundant during the summer months (Blackburn 1979). Major pupping areas appear to be located where food is abundant and varied and is available over a broad period of time.

Causes for the variation in time of pupping should also be looked for in other environmental parameters, such as water temperature and weather, which might affect survival of recently born pups. For instance, in Aialik Bay, a factor affecting pup mortality appears to be the amount and quality of ice available for haulouts. The timing of parturition there is during the period of minimal winds and maximal abundance of ice (Fig. 24). On Sable Island, the timing of parturition was correlated with annual variation in water temperature (Boulva 1975). Latitudinal changes affect a host of environmental parameters, which alone, or in combination, could cause variation in the timing of parturition. Perhaps, a productive approach would be examining areas deviating from the cline, such as Puget Sound, in order to isolate important relationships.

Use of Habitat

In general, the activity rhythms of harbor seals show peak abundance on the haulouts when shorelines are maximally exposed (i.e., at falling and low tides) or when human disturbance is minimal (i.e., at night in industrial areas). Where availability of substrates is not regulated by tides or disturbance, a diel activity rhythm prevails. Diel activity rhythms have been seen in ringed (*Phoca hispida*), harp (*P. groenlandica*), crabeater (*Lobodon carcinophagus*), leopard (*Hydrurga leptonyx*), Weddell (*Leptonychotes weddelli*), and perhaps Ross seals (*Ommatophoca rossi*) in the Arctic and Antarctic, where ice is consistently available for use as haulouts (Finley 1979, Ronald and Healey 1981, Kooyman 1981a, b, c, Ray 1981b). In Aialik Bay, where the most important secondary factors determining the number of seals hauled out were the weather and the abundance and stability of the ice, a diel rhythm also prevailed.

Stirling (1975) and Le Boeuf (1979) proposed several ways in which sea ice might affect life-history strategies of seals. They suggested that predictability in the abundance, location, and quality of sea ice, as well as the virtually unlimited access to the surface of the ice, would affect seals in at least three ways: (1) increased distances between individuals, (2) increased synchronization of pupping and breeding, and (3) decreased duration of the suckling period.

The effects of glacial ice on life-history apparently are not quite the same as those of sea ice, to judge from the comparative life-histories of harbor and spotted seals (*Phoca largha*). Pups of the glacial harbor seals are are born without the lanugo coat, prepared to swim at birth, like shore-based harbor seals; thus, they are adapted to use the abundant but short-lived glacial ice. Pups of the spotted seals are born in lanugo, which serves them well as insulation as long as it stays dry; hence, they are adapted to use the comparatively long-lived floes of sea ice. Whereas the mother-pup pair of glacial seals may change locations daily, the spotted seal mother and pup tend to remain for several weeks on the same floe where the pup was born.

In Aialik Bay, female harbor seals with pups tend to minimize their interactions with other seals, particularly at the time of parturition, by selectively hauling out in low density aggregations on bergs not occupied by other seals. Spotted seals give birth on floes separated from other spotted seals by at least 0.25 km; the female and pup share their floe with an adult male which presumably mates with the female (Burns 1970). Mother-pup pairs of glacial seals tend to aggregate more as the pup matures. This tendency is similar to that of female harbor seals on coastal haulouts, which tend to occupy the periphery of mixed aggregations or to use "nursery beaches" when giving birth and caring for young pups (Knudtson 1974, Sullivan 1980) but mix with other age classes to a greater extent as the pup grows (Johnson 1976a,b).

The seasonal variation in the density of aggregations in Aialik Bay shows trends that are in some ways similar to those seen in spotted seals whose haulout space on the pack ice is unlimited. Spotted seals are widely distributed singly and in pairs in the southern part of the pack ice during the pupping season. They leave the ice to breed, but they congregate in groups on ice during the molt and in larger herds on shore summer (Burns 1970, Frost et al. 1982). The glacial seals of Aialik Bay left the pupping area during the breeding season, as do spotted seals. Like the spotted seals, the glacial seals became more gregarious during the molt. The densest concentrations of glacial seals at that time were similar to those of harbor seals on shore. For the molt, the seals using glacial ice may be limited by the amount of space available, like those on shore.

Since wind and ocean currents disperse pack ice, there is strong selection in pagophilic seals for synchronization of parturition during the most favorable weather and most stable ice conditions. There is also strong selection for a reduced suckling period (Burns 1970, Stirling 1975). Premature break-up of the ice may increase pup mortality by exposing dependent pups to the thermal disadvantage from immersion, death from being crushed by moving ice, or starvation from being separated from the mother. Although immersion and crushing appear to be unimportant as causes of pup mortality for glacial seals, unseasonal depletion of ice does appear to have a negative effect on pup survival. During 1979, limited availability of ice while the pups were young forced them to remain in the water for long periods. This probably increased their energy expenditure at a disadvantageous time and increased the potential for permanent mother-pup separations. The increase in lone pups sighted in 1979 and the almost 50% reduction in number of weaned pups that year indicated the importance of haulout areas to those pups while young.

The time of pupping in Aialik Bay coincides with the most favorable ice conditions and moderate winds. The duration of the pupping period from the estimated birth of the first pup to that of the last pup (7-10 weeks) falls well within the range (4-12 weeks) reported for harbor seals pupping on shore in other localities (Bishop 1967, Bigg 1969a, Knudtson 1974, Johnson 1976b) but is more prolonged than that reported for spotted seals (3-6 weeks) on the pack ice (Naito and Nishiwaki 1972, Shaughnessy and Fay 1976, Li 1980). The duration of the suckling period (Table 14) for glacial seals in Aialik Bay more closely resembles that of spotted seals than of harbor seals pupping on shore. The diminution of both

Table 14. Duration of suckling for phocid seals on land and on ice in the North Pacific region.

Species	Habitat	Duration of suckling	Reference
Bearded seal (Erignathus barbatus)	Pack ice	12-18 Days	Burns 1981a
Harbor seal (P. v. richardsi)	Glacial ice	23 Days	This study
Spotted seal (P. largha)	Pack ice	24-28 Days	Li 1980
Ribbon seal (P. fasciata)	Pack ice	21-28 Days	Burns 1981b
Harbor seal (P. v. richardsi)	Land	28-42 Days	Bigg 1969a, Knudtson 1974 Johnson 1976a
Ringed seal (P. hispida)	Fast ice	35-49 Days	Frost and Lowry 1981

glacial and pack during the nursing period may exert a strong selective influence to minimize the duration of the mother-pup bond.

In conclusion, glacial harbor seals apparently show some ecological responses specific to the ice substrate, which are not generally seen in harbor seals on shore. Bartholomew (1970), Stirling (1975), and Le Boeuf (1979) argued that suitable haulout areas on shore are limited, and seals are forced to congregate in the space available, which, in turn, strongly affects their social organization. Given abundant and more or less persistent haulout space, away from terrestrial predators, the harbor seals in Aialik Bay continue to aggregate, albeit in lower densities than for seals on shore.

Selective Advantages of Ice as a Haulout Substrate

The use of glacial ice by harbor seals in the North Pacific is limited geographically to a few fjords in the Gulf of Alaska. In those locations, the harbor seals appear to haul out on the ice in preference to hauling out on shore (Streveler 1979). The harbor seals in southeastern Bering Sea and in a few other northern areas in the Gulf of Alaska also seem to prefer to use sea ice whenever it is available to them, rather than their usual coastal sites (F. H. Fay, pers. comm.). Fay (1974) has suggested that there may be several ecologically important reasons for selective use of ice by pinnipeds:

Isolation. In their selection of sites on which to haul out, most pinnipeds choose isolated islets and offshore rocks, rather than the continental coasts or larger islands (Scheffer 1958, p. 7). The basis for this selection seems obvious: these isolated sites provide the best refuge from predators and other disturbing terrestrial mammals. In this respect, ice provides equal or better isolation than can be found in most terrestrial sites.

Space. The ice pack provides an enormous number of isolated islets that vastly increase the space available for pinnipeds to haul out. Many more animals are accommodated than would be feasible on the few terrestrial islets extant in the Bering Sea.

Variety. The variety of "terrain" provided by fast ice, moving ice, large and small floes, thick ice, thin ice, brash, and open water favors diversity of occupants and preferential selection of habitats. More species may be accommodated on ice than could be accommodated on land.

Food supply. For the benthic feeders in particular, the presence of ice over the entire Beringian intercontinental shelf provides easy access to a much greater and more varied food supply than would be available to them from the shores and islands. This also provides for significantly larger populations than could be supported in the absence of ice.

Transportation. Those species that inhabit the moving ice are continuously transported to new feeding areas in a passive way, which helps to distribute more evenly their influence on the sub-ice communities. This is particularly true of the benthic feeders. Much energy is conserved as a consequence of this transportation, for the animals are seldom obliged to swim to new feeding areas, and those in migration are often carried much of the way by the ice.

Sanitation. Many of the known diseases and parasites of pinnipeds are favored by crowding and continuity of site occupation. Since it is seldom necessary for pinnipeds to crowd together on the ice or to occupy the same floe more than once, the conditions for transmission of such diseases and parasites are unfavorable.

Shelter. The hummocks of pressure-ridged ice not only interfere with the predators' view but also effectively reduce wind velocity and the general severity of the weather at the seals' level. The young of the _largha_ seal

> and harp seal take refuge from intruders and the weather among the ice blocks of a pressure ridge, while the young ringed seal is protected by a snow cave on the ice.

Because glacial ice differs from sea ice in several respects, not all of the suggested advantages are applicable. Glacial ice is less diverse and expansive than sea ice, and does not offer the same attributes of greater food supply, transportation, or shelter. The areas covered by glacial ice are small, and are generally confined to the vicinity of the tidewater glaciers. The seals apparently do not use glacial ice once it has been moved out of the fjords by surface currents and winds. Since the glacial ice is concentrated in the same small areas each year, the seals also concentrate there. The short "lifespan" of most of the glacial ice (on the order of hours, rather than months) also reduces the probability of the seals being transported significantly. To feed, the seals appear to leave the ice-covered area and swim to the open sea or outer parts of the fjords. Glacial ice also does not offer the wide variety of "terrain" for haulouts as seen in sea ice; evenso, the seals do have some latitude in the selection of bergs. Females giving birth and rearing pups tend to select larger bergs than do the other age classes. The topography of even the large bergs offers little shelter from adverse weather, but the presence of rafted glacial ice does damp the effects of chop and swells. Glacial ice usually occurs in deep fjords, which provide some shelter from the adverse coastal weather. When foul weather affects the fjords, the seals tend to abandon the ice until the storm abates. On both sea ice and glacial ice, tides have little or no influence on the amount of surface area available for haulout.

The seals appear to have less difficulty in hauling out on ice than on shore, and this is especially beneficial for young pups (Sullivan 1980). The surface irregularities of the bergs provide a wide assortment of sites suitable for seals of all ages. Seals climbing out of the water easily pull themselves onto the bergs by grasping the rough, cracked surface with their claws. Their hauling out also is facilitated by the calm waters around the bergs; seals hauling out on rocks and beaches often are hindered by surf and the slippery surfaces of the rocks (Johnson 1976a, Sullivan 1980). In Aialik Bay, I observed that pups and even some adults had difficulty in climbing out on the algae-covered rocks. In a few instances, a pup eventually gave up and swam away, whereupon its mother also abandoned the rocks and followed. When hauled out on the rocks, the pups occasionally were swept off into the water by waves. Often, the seals swam near offshore rocks and islands in the upper bay, but they seldom attempted to haul out.

SUMMARY

The Pacific harbor seal (_Phoca vitulina richardsi_) is an ecological generalist which occupies diverse nearshore habitats. One of the most unusual of those habitats is rafted ice from tidewater glaciers. The social behavior and life-history of phocid seals vary with the kinds of substrates that they use for haulouts. Seals hauling out on shore tend to be more gregarious than those hauling out on sea ice. Glacial ice has characteristics intermediate between sea ice and shore. The objective of this study was to examine some of the effects of glacial ice on the life-history of the Pacific harbor seal and to compare the life of these glacial seals with that of harbor seals in other habitats.

The study was conducted in Aialik Bay, southcentral Alaska, from 1979-1981. Field camps were occupied on the Bay between mid-May and mid-August in 1979 and 1980 and from late May to mid-June in 1981. Mid-winter surveys were conducted during the first week of December in 1979 and 1980. Data collected included information on numbers, age composition, aggregation characteristics, substrate selection, general behavior of the seals, and the availability of suitable prey in the area.

The use of glacial ice as a haulout varied with environmental conditions and with stages in the life-history of the seals. The abundance of seals on the ice was highest in midday from 1100-1500 h during days of fair to overcast weather, especially on the first and second day following a storm. Fewest seals were hauled out at night

and during periods of strong winds (> 10 m/s). Seal numbers also were low when ice covered less than 6% of the area north of Slate Island and on the day preceding a storm. Tides had little effect on the number of seals hauled out.

The numbers of seals on the ice changed throughout the spring and summer. Highest counts of up to 1,633 seals were obtained in mid-June, during pupping, and in August, during the molt. Fewest seals hauled out in May prior to pupping and in July, during the breeding period.

Parturition occurred from early May to mid-July. Greatest numbers of pups were born from 4-7 June. The nursing period was estimated at 23 days. Temporary separations of mother and pup takes place frequently in the week prior to permanent termination of the mother-pup bond.

In 1979, up to 50% of the pups were separated from their mothers prematurely and may have died as a consequence. This took place when strong northwesterly winds, dispersed the ice out of the bay for several days when most pups were less than one week old.

Breeding was estimated to take place from the third week of June to the first week of August and to be most frequent in the first week of July. Two possible instances of breeding, one within and one away from the ice, suggested that more than one breeding strategy may be used. Within the ice, a male in the water appeared to defend a "mobile territory" adjacent to an aggregation of seals on the ice.

I saw seals that were shedding hair in the molt from 16 July to the end of observations in mid-August. The greatest proportion of seals showing 1-50% hairloss was seen on 5 to 8 August; the proportion with hairloss decreased therafter. After completing the molt, the seals apparently left the area.

During pupping/nursing periods in June, adult seals comprised 60%-90% of the seals hauled out; in July and August, during breeding and molting periods they comprised less than 30%. Subadults represented over 80% of the seals during the molt. Most adults did not appear to molt in Aialik Bay, perhaps because of unpredictable and often limited haulout space.

Seals of different reproductive categories tended to segregate. Seals without pups hauled out mostly in midday on bergs 1-5 m in surface diameter, <4 m from the nearest occupied berg. About 40% were on a berg with at least one other seal. Haulout sites were mostly in 7- to 8-okta ice.

Seals caring for pups were less gregarious, hauling out earlier in the day on larger bergs and farther from other occupied bergs, also in 7- to 8-okta ice. Only 8% of these seals shared their bergs with other seals. Females with pups shared bergs most often with other seals in July (the breeding period) when disproportionately more adults were on those bergs than represented in the population resting on the ice.

Females giving birth selected the most stable ice with the least potential for disturbance. Births took place mainly in the evening and early morning (least often in midday), on large bergs (>5 m in diameter), more than 8 m from other seals, and in 8-okta ice. Females giving birth never shared their berg with other seals.

Little evidence of feeding was seen near the ice. Some apparent feeding was seen along the shoreline and in Pederson Lagoon. The most abundant potential prey in the Bay included: walleye pollock (Theragra chalcogramma), Pacific herring (Clupea harengus), eulachon (Thaleichtys pacificus), and capelin (Mallotus villosus).

Four methods for estimating the population size of harbor seals in Aialık Bay yielded results that differed by an order of magnitude. Systematic aerial and boat surveys consistently underestimated the number of seals in the area. Counts taken periodically during long-term field studies disclosed major changes in composition by age class. Seals counted during the pupping period were mainly adults and pups while those counted during the molt were mainly subadults. Survey techniques presently used to census seal populations are inadequate to detect any but very large changes in the size of populations.

Most populations of harbor seals tend to haul out in greatest numbers when shorelines are maximally exposed by low tides. Seals hauling out on the glacial ice in Aialik Bay, however, were most strongly influenced by diel rhythms, like phocid seals using sea ice.

Harbor seals on glacial ice have life-history characteristics intermediate between those of harbor seals on shore and those of the closely related spotted seal (Phoca largha) of the pack ice. Seals on glacial ice disperse more than seals on shore but aggregate more than spotted seals on sea ice. Pupping takes place over a long period, more like harbor seals on shore, but the duration of the mother-pup bond appears to be short, more like spotted seals on sea ice.

Glacial ice areas attract seals in large concentrations. Ecological factors which may select for the use of ice include (1) isolation from predators and other disturbances, (2) increased space and access to it, (3) protection from foul weather and rough seas, (4) a lesser likelihood for transmission of diseases, (5) greater variety in size and topography of haulout sites, and (6) an easier surface on which to haul out.

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